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Authors

Mahardja, Brian
Bashevkin, Samuel M.
Pien, Catarina
et al.

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STATE OF BAY-DELTA SCIENCE

Heatwaves and Rising Temperatures in the Upper San Francisco Estuary: Trends and Effects on Ecosystems and Humans

Brian Mahardja*[1], Samuel M. Bashevkin*[2], Catarina Pien[1], Shruti Khanna[3†], Dharshani Pearson[4†], Brittany Davis[5], Rupa Basu[4†]

ABSTRACT

Rising temperature is one direct consequence of climate change, and temperature is a key controlling variable on biological processes from molecular to ecosystem scales. While rising average temperature is one of the most discussed aspects of climate change, extreme events such as heatwaves are also expected to increase in duration, intensity, and frequency. These changes will bring about effects that threaten the integrity of the upper San Francisco Estuary (estuary) ecosystem, the services they provide to humans, and the health of humans that reside in the region. In the estuary, warmer temperatures are expected to result in seasonal shifts to life-cycle timing, and to favor smaller-bodied individuals across most non-human taxa. Several native fish species will likely decline, while a considerable number of non-native and cosmopolitan species tolerant of high temperatures are predicted to be relatively unaffected by or even benefit from a warmer climate. For humans, high temperatures and heatwaves are associated with wide-ranging health effects, from direct effects such as dehydration and heat exhaustion, to indirect and adverse health outcomes such as lower birth weight, mental health problems, and violence. These health effects will be exacerbated by ecosystem changes, as a longer warm season will increase our exposure to vectors such as mosquitos, as well as to the toxins produced by harmful algal blooms. Climate change is a global issue that cannot be resolved effectively at a regional level; however, some actions can either be taken or further studied to potentially lessen the effects of rising temperatures for the estuary's ecosystem and residents at a more localized level. Although decreasing global greenhouse gas emissions remains our best option to combat climate change and the resultant temperature increases, successful adaptation to warming and heatwaves will require actions at multiple scales.

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* Co-first authors and corresponding authors: *bmahardja@usbr.gov*, *sam.bashevkin@waterboards.ca.gov*

1 US Bureau of Reclamation, Bay-Delta Office
Sacramento, CA 95814 USA

2 California State Water Resources Control Board
Sacramento, CA 95814 USA

3 California Department of Fish and Wildlife
Stockton, CA 95206 USA

4 California Office of Environmental Health Hazard Assessment, Community and Environmental Epidemiology Research Branch
Oakland, CA 94612 USA

5 California Department of Water Resources
West Sacramento, CA 95691 USA

† *These authors contributed equally, and author order was selected randomly*

KEY WORDS

California, climate change, temperature, heatwave, estuary, ecosystem, health, epidemiology

INTRODUCTION

Climate change is a global phenomenon that is affecting human societies and ecosystems. One direct consequence of climate change is an increase in temperature, a controlling variable on biological processes from molecular to ecosystem scales (Petchey et al. 1999; Clarke 2006; Parain et al. 2018). A warmer biosphere comes with a litany of cascading effects, which threaten the integrity of ecosystems and the services they provide to humans. While rising average temperature is one of the most studied and discussed aspects of climate change, extreme events such as heatwaves are also expected to increase in duration, intensity, and frequency. Indeed, higher frequency of extreme warm events can already be observed in the recent historical record (Seneviratne et al. 2014). These "heatwaves" are generally associated with prolonged periods of exceptionally high temperatures, though the term itself does not have a universally accepted formal definition. Nevertheless, the human health issues and ecosystem effects of past extreme heat events are already apparent and may become more severe in the future (Parmesan et al. 2000; Ciais et al. 2005; Robine et al. 2008).

California plays a prominent role in the economy of United States and worldwide (*https://apps.bea.gov/regional/bearfacts/?f=06000&a=3*), and as such, there is much interest in assessing the existing and expected effects of climate change-related extreme events in the region. This interest is especially true for the Sacramento–San Joaquin Delta (Delta), the central hub of California's water supply that greatly influences the state's economy and biodiversity. Once a landscape of expansive tidal wetlands, the Delta has been transformed into a series of channelized rivers and open waterbodies for agriculture and water conveyance (Whipple et al. 2012). Today, water from the Delta is used by 27 million people and for ~18,000 km^2 of farmland throughout California. The Delta region also contains several cities as well as significant farmland, with over 500,000 residents within the Delta, and many more people in adjacent cities (e.g., Sacramento adds another 520,000 people and Stockton adds another 320,000 people). The Delta is also home to a variety of plant and animal species, some of which are both native and endemic (i.e., not found elsewhere). As a result of habitat alteration and other anthropogenic effects that have accumulated in the Delta ecosystem over time, several native species in the Delta have experienced severe declines. Conflicts in water-management priorities in the Delta grew as these native species declined, some became listed under the federal and state Endangered Species Acts (ESAs), and the ecosystem continued to deteriorate (Luoma et al. 2015). Except in the wettest years and months, California water supply is over-allocated, without enough supply to fully satisfy demands from agricultural, municipal, industrial, and environmental uses.

It is within this context of limited water and conflicting priorities for water that increasingly warmer temperatures and extreme heat events may alter the Delta ecosystem—from affecting its food-web dynamics, to reducing habitat quality for species of concern and increasing the risks for future species invasions (Herbold et al. 2022). For communities that rely on the water and ecosystem services that the Delta provides, heat is also one of the biggest health hazards (Guirguis et al. 2014). The magnitude of these hazards was apparent in 2006, when a California heatwave resulted in possibly more than 600 deaths (Ostro et al. 2009) and over 16,000 emergency hospital visits (Knowlton et al. 2009) across the state. Meanwhile, demographics are rapidly changing in the area, increasing the complexity of the public health response and messaging to vulnerable human populations as we attempt to adapt to climate change.

Understanding the potential future behavior of ecosystems and the effects on humans from both the warming trend and extreme climate events can help guide strategies to cope with such climate change effects (Jentsch et al. 2007). Here we synthesized past research and analyzed existing data to better describe temperature trends and the frequency of heatwave events in the upper San Francisco Estuary (estuary), as well as summarize their potential ecological and human effects. We first describe recent temperature patterns and extreme heat events to provide context on the current trajectory of the system. We then review the literature on ecological and human effects of rising average and extreme temperatures. Lastly, we provide considerations for resource management, adaptation strategies, and scientific research.

Although temperature issues permeate the entire watershed from California's Coastal, Cascade, and Sierra Nevada mountain ranges to the San Francisco Bay, we will focus our efforts on the upper estuary, including the legal Delta, Suisun Marsh, and Suisun Bay (Figure 1), where:

- The climate is Mediterranean, with wet, mild winters and hot, dry summers
- A critical node of California's water infrastructure can be found
- Land subsidence and a weakening levee system threaten scarce freshwater availability for an agricultural powerhouse and many key municipalities;
- A highly altered and invaded aquatic ecosystem and hydrological modification have caused significant declines to native fauna and productivity
- Demographics are rapidly changing, increasing the complexity of the public health response and messaging to vulnerable human populations as we attempt to adapt to climate change

Our goal is to identify key effects and uncertainties that surround heatwaves and rising temperatures in the upper estuary, which can subsequently be used to develop adaptation strategies and tools to manage such effects.

TRENDS AND DRIVERS OF TEMPERATURE

Temperature Drivers

Air Temperatures

Air temperatures are primarily driven by atmospheric influences such as solar radiation (which is in turn driven by seasonality, cloud cover, and aerosols such as wildfire smoke) and weather (Figure 2). Proximity to the Pacific Ocean heat sink somewhat buffers seasonal to decadal air temperature variability in the Delta compared to other parts of North America, particularly the continental interior. However, heatwaves are still common in the Delta, and they come with a variety of effects (Dettinger et al. 2016). To evaluate effects, it is important to consider the metric of temperature exposure—such as daytime maximum, nighttime maximum, and mean— as well as exposure length, including cumulative short-term or long-term exposures. Urban areas are generally more prone to heat exposure because of the urban heat island effect, which refers to more retention of heat in cities where there is more asphalt and cement, and less greenspace (Tuholske et al. 2021). Another metric to consider when assessing the effects of heatwaves is apparent temperature (also known as the heat index or humidex), a combination of the air temperature and relative humidity to depict what the human body actually feels.

In the estuary, a few local phenomena can exert large influences on temperatures. The Delta Breeze is a sea breeze that penetrates into the Central Valley through Carquinez Strait in the warmer months and can exert a strong cooling effect on Delta air temperatures (Hayes et al. 1984). This breeze phenomenon primarily occurs from late spring through early fall, and is strongest and most frequent during the summer (Zhao et al. 2020). Hayes et al. (1984) detected Delta Breezes in 72% of evenings from May to September in Davis, California, near the northwestern Delta, which resulted in cooling of up to 6 °C compared to days without Delta Breezes. On average, Delta Breezes result in cooling of 3 °C in the Bay Area, 1.5 °C in the Sacramento Valley, and 0.4 °C in the San Joaquin Valley (Zhao et al. 2020).

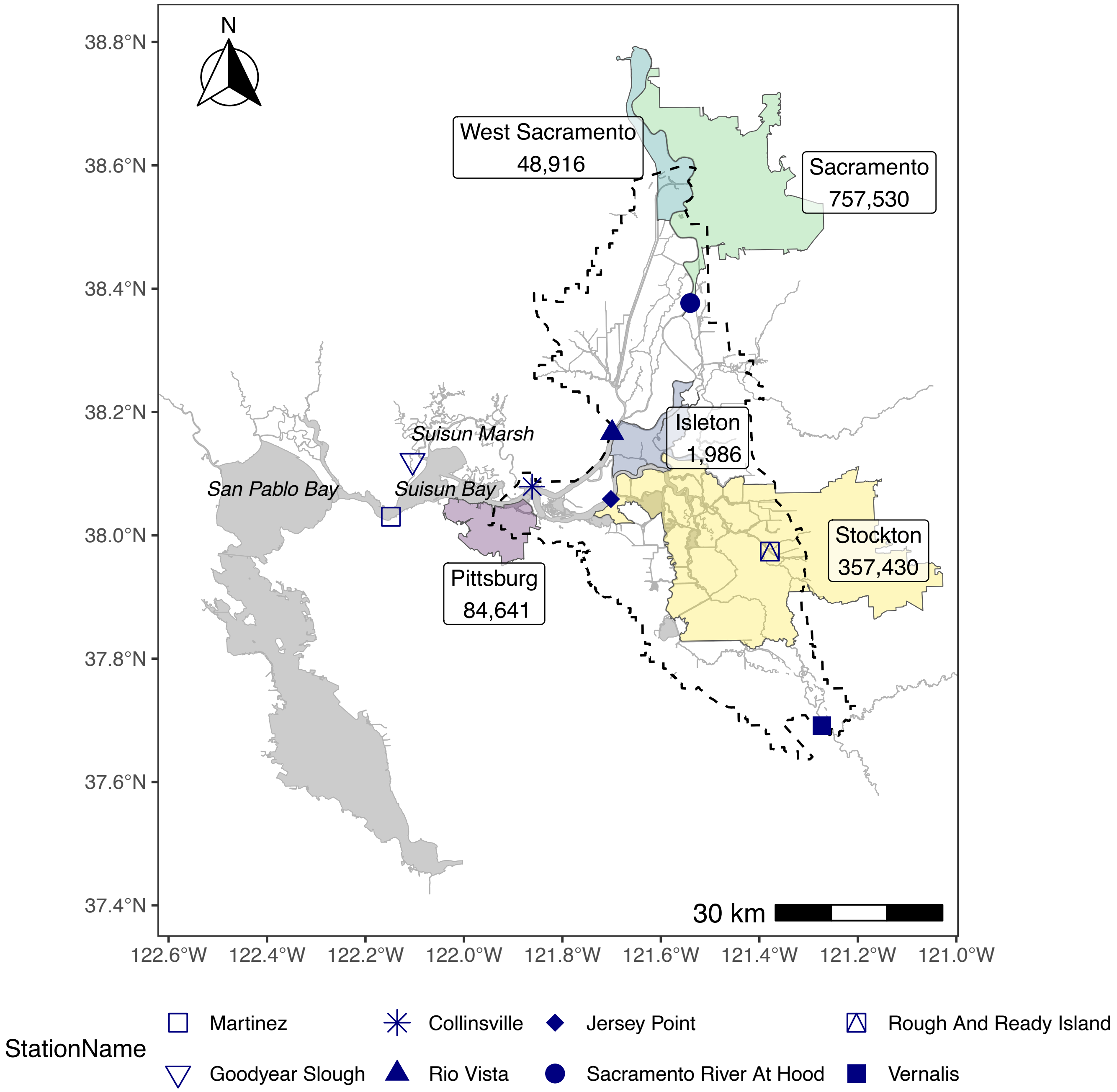

Figure 1 Map of the study area (Suisun Bay, Suisun Marsh, and the Sacramento–San Joaquin Delta). *Shaded shapes* and corresponding labels indicate cities selected for the air temperature heatwave analyses. The *shaded area* encompasses the area of every ZIP code that falls at least partially within the city limits. However, air temperature and humidity data were extracted from the population weighted centroids of each ZIP code. Numbers under the city name represent the approximate populations within the shaded ZIP codes. Populations and zip code boundaries were obtained from the zipcodeR package for R (Rozzi 2021). *Points* indicate stations selected for the water temperature heatwave analyses. The *dashed black line* indicates the boundary of the legal Delta.

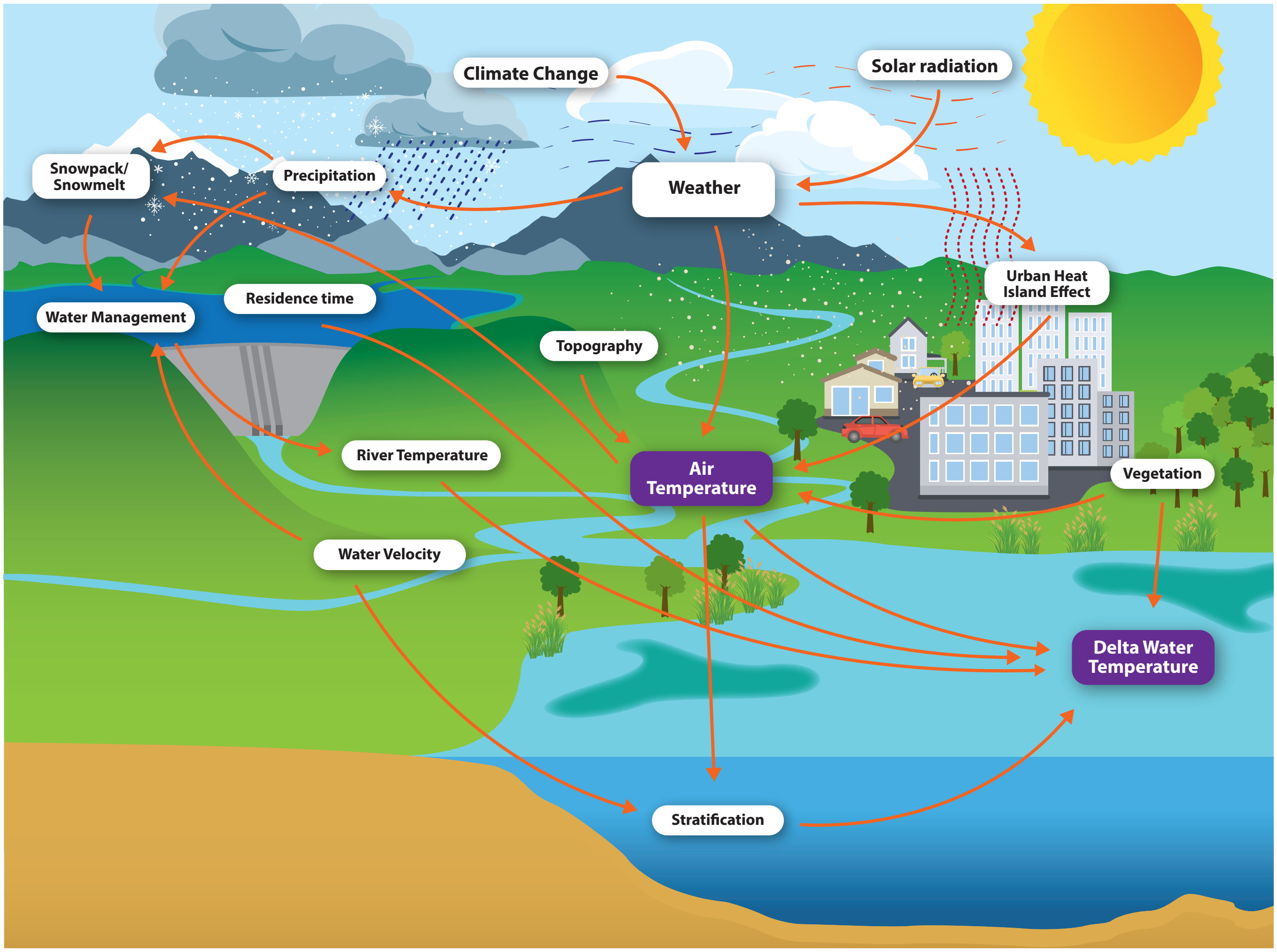

Figure 2 Conceptual model of factors that drive air and water temperature in the upper estuary. Credit: Illustrated by Vincent Pascual with the California Office of State Publishing.

In the summer, the Central Valley regularly develops a subsidence inversion, in which warmer air overlies relatively cooler air (Zhong et al. 2004; Grotjahn 2011). This phenomenon can trap a layer of air close to the surface, increasing the effect of solar radiation on surface air temperatures, and also trapping air pollution and reducing air quality (Grotjahn 2011). Subsidence inversion is associated with the hottest days in the Central Valley, with high nighttime temperatures, and offshore winds that can oppose or restrict cooling sea breezes (Grotjahn 2011), such as the Delta Breeze. Although the strength of these inversion layers is expected to increase with climate change, lower heights of the base inversion layer are more strongly associated with coastal heatwaves, and the evidence for future changes in base inversion height is less clear (Clemesha et al. 2018).

During the wet season, atmospheric rivers cause almost all of the most extreme precipitation events in California (Dettinger 2011; Dettinger et al. 2016). In addition to bringing significant precipitation, atmospheric rivers also bring warm temperatures. From December through February, days with atmospheric river events in California average 1.8 °C warmer than days without (Dettinger 2011).

Fog can also influence temperatures in the Central Valley. In particular, Tule Fog is a radiative fog that forms in winters when storms create enough humidity to form fog during long periods of high pressure. Thus, it occurs less often during droughts, when humidity is lower, and at intermediate levels in the wettest years, which have too many storms to develop the required long period of high pressure (Baldocchi and Waller 2014). During foggy days in the Central Valley, daily maximum air temperature is 7 °C cooler on average (Baldocchi and Waller 2014). From 1981 to 2014, fog occurrence decreased by 46% (Baldocchi and Waller 2014).

Water Temperatures

Water temperatures in the upper estuary are primarily driven by atmospheric influences, including air temperature, humidity, and cloud cover, with some effect of riverine inflows (Figure 2). Ocean temperatures have a negligible effect in the Delta because the tidally exchanged water has already equilibrated with atmospheric conditions (Wagner et al. 2011; Vroom et al. 2017). However, atmospheric influences can cause temperature changes of up to 10 °C in the summer in the Central Delta. Among the individual atmospheric components, humidity has a positive effect on water temperatures because of its inhibition of evaporative cooling, with differences of up to 10 °C from the lowest to highest recorded humidity values (which wouldn't necessarily occur in the same season, so this is not directly comparable to the overall maximum atmospheric effect of 10 °C mentioned above). Cloud cover has a cooling effect on water temperatures because of the reduction in solar radiation, with changes of up to 5 °C from the lowest to highest cloud cover value. Lastly, air temperatures have a positive effect on water temperatures, and a 10 °C difference in air temperature can induce a 7 °C change in water temperatures (Vroom et al. 2017). Atmospheric heat exchange increases water temperatures in most of the Delta, except near the San Joaquin River input, where atmospheric heat exchange can lower water temperatures (Vroom et al. 2017).

The effect of inflow on water temperatures in the Delta is still, to some degree, an open question, with contrasting statements in the literature (reviewed in Bashevkin and Mahardja 2022). Some studies have suggested that reservoir-released inflow (i.e., the majority of inflow: Kimmerer 2004; Brown and Bauer 2010) and snowmelt have a limited influence on water temperatures in the Delta (Cloern et al. 2011; Sommer 2020), and one study found a greatly reduced influence of Keswick dam discharge volume and temperature on water temperatures in the Sacramento River before it reaches the Delta (Daniels and Danner 2020). In contrast, other studies have found negative relationships between temperature and inflow (Kimmerer 2004; Wagner et al. 2011; Jeffries et al. 2016; Munsch et al. 2019; Nobriga et al. 2021; Bashevkin and Mahardja 2022). Bashevkin and Mahardja (2022) found predominantly negative relationships between temperature and inflow, with differences of up to 2 °C between high- and low-inflow years. However, in the winter months and in the Confluence and Suisun regions from July through September, there was a positive relationship between temperature and inflow, with differences up to -1.2 °C between high- and low-inflow years. Nevertheless, it is important to note that this study neither evaluated causality nor isolated effects of dam releases. Lending further credence to an inflow–temperature relationship in the Delta, Vroom et al. (2017) found that lower residence times reduce the strength of the atmospheric influence, such that water temperatures near the river inputs (where residence time is shorter) are less affected by atmospheric influences and more affected by the river inflow temperature (Vroom et al. 2017). They found that discharge reductions of 33% could increase temperatures up to 2 °C near river inputs. Although some evidence indicates that inflow can influence water temperatures in the Delta, further analysis is needed to estimate the strength of that effect at a seasonal time-scale and tributary spatial scale. This would enable an evaluation of the effectiveness and water cost of any potential Delta temperature-management actions.

Water temperatures can also be influenced by more localized factors such as tidal exchange with shallower waterbodies, vegetative shading, or vegetative influences on residence time (i.e., the amount of time a parcel of water remains in a given location). Shallower, inundated areas such as wetlands are more strongly influenced by atmospheric influences than deeper waterbodies. Thus, when wetlands are flooded during cooler parts of the day (such as the night), this water can cool more rapidly than the open channel, so when it eventually drains into a nearby channel, the process can exert a cooling influence. Enright et al. (2013) detected this effect, finding that the highest (spring) high tides in the summertime coincide with the late evening, allowing marshes to act as heat sinks during these times. However, the timing of these highest (spring) high tides is dependent on a 335-year cycle set to invert in about 160 years, which will lead the marshes to flood during the daytime instead of nighttime in the summer. As a result, this reversal could exacerbate consequences of heat events by causing marshes to act as a heat source during summertime spring high tides.

More consistently, riparian vegetation reduces water temperatures by blocking solar radiation. The complete removal of all riparian levee vegetation in the Delta was estimated to increase incident solar radiation by 9%, which could result in a Delta-wide temperature increase of 0.1 °C with localized increases up to 14.3 °C on cloudless days (Greenberg et al. 2012). Lastly, aquatic vegetation can affect water temperatures in two contrasting manners: it can increase residence time and thus increase water temperatures through increased exposure to atmospheric influences, or it can shade the water column and thus decrease water temperatures (Tobias et al. 2019). Because of these contrasting influences, the net effect of aquatic vegetation on water temperatures in the Delta is unclear and merits further study.

Past Changes

Temperature Trends

Both air and water temperatures have increased in the estuary in the recent past. From 1901 to 2010, average annual air temperatures in the southwestern USA have warmed by 0.008 °C yr^{-1}, while increases in the estuary have ranged from 0.009 to 0.016 °C yr^{-1} (Hoerling et al. 2013). Average water temperatures in the estuary have also increased at generally similar rates (Bashevkin et al. 2022: 0.017 °C yr^{-1} from 1969 to 2020; Shellenbarger and Schoellhamer 2011: 0.007 °C yr^{-1} from 1985 to 2001), with a more rapid rate for annual maximum water temperatures at 0.1 °C yr^{-1} from 1985 to 2019 (Halverson et al. 2022). Long-term water temperature increases exhibited spatial and seasonal variability. Seasonally, the greatest temperature increases were found in the late-fall to winter (November–February) and mid-spring (April–June) and spatially the greatest temperature increases were found in the northern Delta (Bashevkin, Mahardja, et al. 2022). Furthermore, the rate and direction of water temperature change has varied over time. In analyzing overlapping 25-year periods from 1970 to present, Bashevkin et al. (2022) found that overall magnitudes of changes (both positive and negative) in each 25-year period were generally greater than the trends over the full 51-year period. Furthermore, some 25-year periods had water temperature decreases—although increases were predominant—and the most recent 25-year period had the most consistent temperature increases.

Heatwave Analysis

Since prior literature on past heatwave trends in the Delta was not available, we conducted an analysis using long-term monitoring data. We used historical water and air temperature data to examine patterns in heatwave frequency, intensity, and duration over the past 2 decades (2002–2022 for water temperature; 1999–2022 for air temperature).

We obtained daily maximum air temperature and daily maximum and minimum relative humidity data from the GRIDMET dataset of ~4-km gridded meteorological data (Abatzoglou 2013). Values were obtained at the ZIP code population-weighted centroids. Average relative humidity was approximated as the midpoint between the daily minimum and daily maximum relative humidities. We then filtered the temperature and humidity data to the ZIP codes from five cities across the Delta (Stockton, Sacramento, West Sacramento, Pittsburg, Isleton; Figure 1) using the package zipcodeR (Rozzi 2021). Within each city, we calculated the maximum daily temperature value and mean daily humidity value. Lastly, we calculated apparent temperatures from the maximum air temperature and average relative humidity data using equations from Basu et al. (2008). These apparent temperatures were used to represent air temperatures in the remainder of this section.

We obtained raw water temperature data from the California Data Exchange Center (CDEC), which hosts continuous water-quality data collected by different agencies. We selected eight stations (Figure 1; see Appendix A, Table A1) that spanned the Delta and the upper estuary, and converted data to an hourly time-scale and removed erroneous data according to IEP et al. (2020). We calculated daily maximum values from these hourly temperatures. There were 1,341 missing values (2.1%) in the maximum water temperature time-series across the eight stations. These gaps resulted from sensor outages or data-quality issues and ranged from 1 to 148 days in length, although most gaps had a short duration. We used the imputeTS package for R to impute series of missing values up to 3 days in duration, using an exponential-weighted moving average. After imputation, 760 missing values (1.2%) remained across the eight stations.

For both sets of data, we calculated daily maximum temperatures for each location. Other studies have used quantiles to characterize heatwaves (Schwarz et al. 2021); thus, we examined 90th, 95th, and 99th quantiles of maximum water temperature across years for each ordinal day and location. We calculated the quantiles within a 31-day window (15 days before and after the given ordinal day) across all years in the dataset. We found that the 90th quantile represented an appropriate number of heatwave events for statistical analyses, and thus defined a heatwave as 3 or more contiguous days where the daily maximum temperature exceeded the 90th quantile. Note that the analysis was intended to inform on a comparative basis the seasonal and interannual trends in heatwave frequency, intensity, and duration, but the values in the results depend on the specific choice of heatwave definition. While some studies have defined heatwaves only during warmer months (Schwarz et al. 2021; USEPA 2024), we believe that heatwaves can apply to aquatic organisms year-round, influencing spawning timing, growth, migration, and other processes (Brown et al. 2016; Kimmerer et al. 2018; Munsch et al. 2019; Goertler et al. 2021; Smith and Nobriga 2023). We classified each data point as either a heatwave or not a heatwave, then calculated, for each station, the proportion of days across months and years that were classified as a heatwave. We also calculated the intensity of each heatwave by dividing the maximum daily temperature by the 90th quantile temperature. To evaluate whether the frequency of heatwaves has changed over time, we ran separate ordinary least-squares linear models with year, location, and the interaction of year and location as covariates for air and water data. The interaction term was not significant for both models, and models without the interaction term were preferred by AIC, so we removed the interaction term from the final models. This analysis was a cursory evaluation of whether trends in heatwave frequencies already exist in the current dataset, and provided additional visualizations for the datasets. Analysis and visualizations were conducted with the R statistical programming language (R Core Team 2023).

For **air temperature**, mean ± standard deviation of 90th quantile temperatures across cities ranged from 17.0 ± 1.17 °C in December to 44.1 ± 1.52 °C in July (Figure 3). The 90th quantile temperature cut-off for air temperature stations generally increased from west to east, reflecting the cooler conditions of cities that are closer to the Pacific Ocean (Figure 3). On average per city, 97 heatwave events—spanning 395 days—were detected across the 24-year dataset, ranging from 89 heatwaves (381 days) in Isleton to 104 (411 days) in West Sacramento. Heatwave frequency was greatest in February and March and in 2017 and 2022 (Figure 4). Heatwave intensity averaged 1.09 ± 0.07 (i.e., 1.09 times the 90th quantile temperature) and was greatest in February and December (Figure 5) and in 2008 and 2021, though intensity among cities was not always consistent (Figure 6). Heatwave duration averaged 4.07 ± 1.74 days and was greatest in January and February (Figure 7) and in 2004, 2005, and 2018, with variation among cities (Figure 8).

For **water temperature**, mean ± standard deviation 90th quantile temperatures across stations ranged from 11.5 ± 0.7 °C in January to 25.1 ± 2.0 °C in July (Figure 3). Aside from Goodyear Slough (a dead-end slough within the Suisun Marsh complex), the 90th quantile temperature cut-off for water temperature station generally increased from downstream (west) to upstream (east), as was observed for air temperature (Figure 3). On average per location, there were 63 heatwaves events that spanned 395 days, ranging from 301 heatwave days (53 events) at Rough and Ready Island to 492 heatwave days (65 events) at Sacramento River At Hood over the 20-year period. Heatwave frequency was greatest in February–March and June–August, and in 2014–2015, 2020 and 2022 (Figure 4). Heatwave intensity averaged 1.04 ± 0.04 (i.e., 1.04 times the 95th quantile temperature). There were no consistent seasonal (Figure 5) or interannual (Figure 6) trends in intensity. Heatwave duration averaged 6.23 ± 4.21 days and was greatest in January, March, and December (Figure 7) and in 2006 and 2015 with variation between stations (Figure 8).

We found a significant trend of increasing frequency of heatwaves by year for air ($p = 0.0002$; increase of 0.4 days per year; Table A2) and water ($p < 0.0001$; increase of 1.2 days per year; Table A3) temperature. This trend might be better defined by an analysis of a longer historical dataset, and may also become more apparent into the future. The frequency and duration of water heatwaves appear to be higher in more recent drought years (2014, 2015, 2021, 2022), which may relate to water-temperature dynamics in the upper estuary being influenced by flow or flow-related factors (Bashevkin and Mahardja 2022).

Overall, heatwave occurrence appears to be more frequent in the winter, early spring, and summer periods (January–March, June–July). Similarly, Bashevkin et al. (2022) found water- temperature increases to be most widespread in winter and mid-spring. Rising temperatures and more frequent heatwaves in the colder parts of the year can negatively affect cold-water native species in the estuary's ecosystem (see "Ecological Effects" below), and may harm the agricultural industry due to growth reduction and chilling requirements of certain crops (Pathak et al. 2018). Rising temperatures and more frequent heatwaves in the summer are likely to further challenge species (e.g., ESA-listed fishes) that already reside in habitats close to their temperature thresholds (Pien et al. 2024). Heat-related health effects are often observed in the summer, but also in the fall, winter, and spring because people are often not acclimated to heat during these seasons (see "Human Effects"; Schwarz et al. 2020).

Future Projections

Climate change is expected to continue increasing temperatures and the frequency and intensity of heatwaves. Air temperatures in the Bay–Delta watershed are expected to increase 0.014 to 0.042 °C yr^{-1} from 2010 to 2099, depending on the climate-change scenario. Over the same time- period, water temperatures are expected to increase at a slightly slower rate than air temperatures, by 0.011 to 0.032 °C yr^{-1} (Cloern et al. 2011). While most of California is expected to experience increases in the intensity, duration, and frequency of air temperature heatwaves by the 2050s, they are not expected to increase in the estuary, potentially because of expected increases in the frequency and intensity of Delta Breeze, which could mitigate temperature increases, particularly in the nighttime (Zhao et al. 2020).

Ecological Effects

Increases in temperature, variability, and extreme heatwave events (including frequency, intensity,

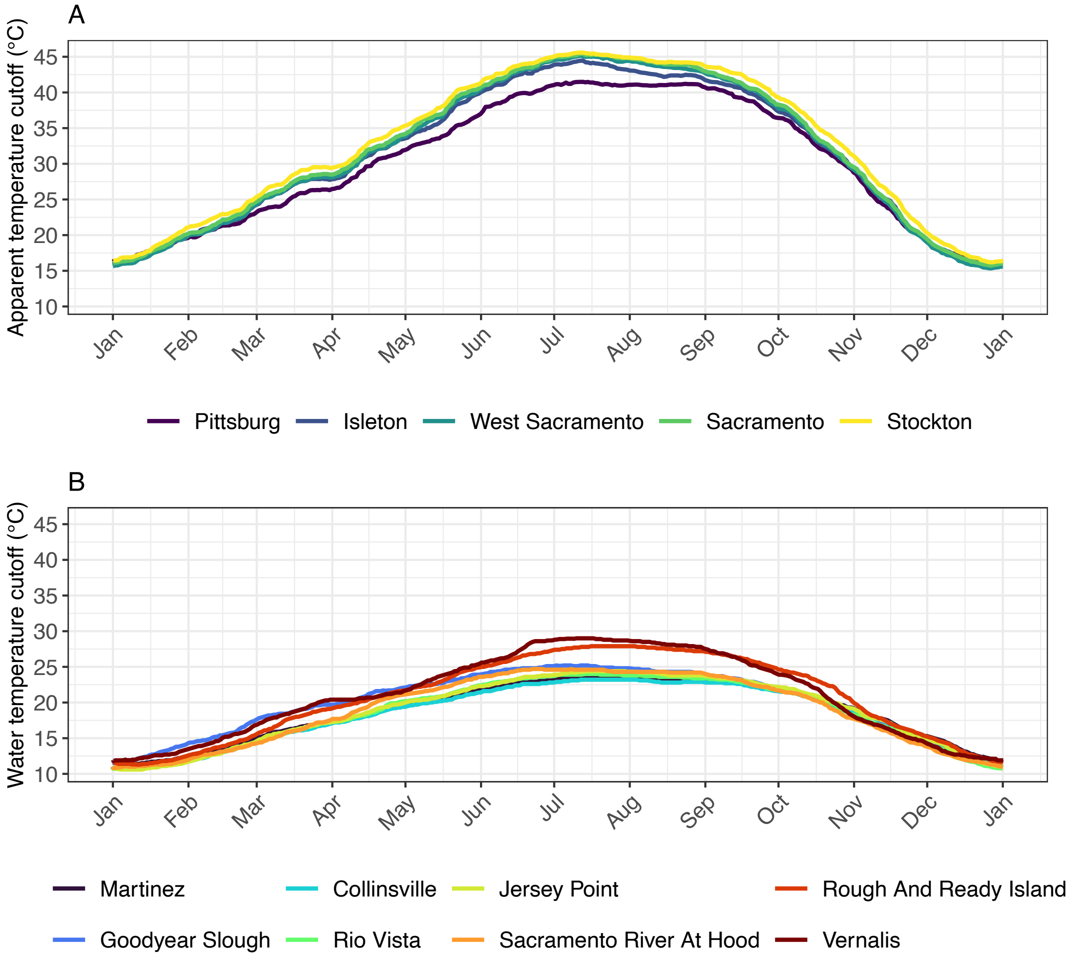

Figure 3 Temperature cutoffs defined by the 90th quantile for each day of year and location. Locations are ordered from West to East.

and duration) are predicted to have cascading and interacting effects on estuarine ecosystems (Scavia et al. 2002; Herbold et al. 2022). Temperature can influence ecological patterns of species distributions and performance, changes in community dynamics, and overall ecosystem functions (Stralberg et al. 2009; Albouy et al. 2014; Wang et al. 2020). Common ecological responses by organisms to climate-driven temperature shifts will likely hold true for the Delta. Phenological shifts across different trophic levels have already occurred (Asch 2015; Merz et al. 2016; Goertler et al. 2021) and will be even more widespread as overall temperature continues to rise (Figure 9). Because of its temperate climate, California hosts a number of species adapted to cooler temperatures (e.g., fish with physiological optimum <22 °C) (Loarie et al. 2008; Moyle et al. 2013). Rising temperatures will favor warmwater or heat-tolerant species across taxa, which are disproportionately made up of introduced species in the Delta. Warmer conditions will also increase the likelihood of additional species invasions across multiple taxa. Aquarium trade and water gardens often use non-native warmwater species that will become more likely to spread as California's climate becomes more habitable to such species. As temperatures become more extreme and unsuitable for many native Delta species, they may adapt by altering their distribution if possible (e.g., to cooler waters downstream, other estuaries for migratory species, etc.). At a longer time-scale, we can also expect to see more species intruding from lower latitudes. The accumulation of these changes will

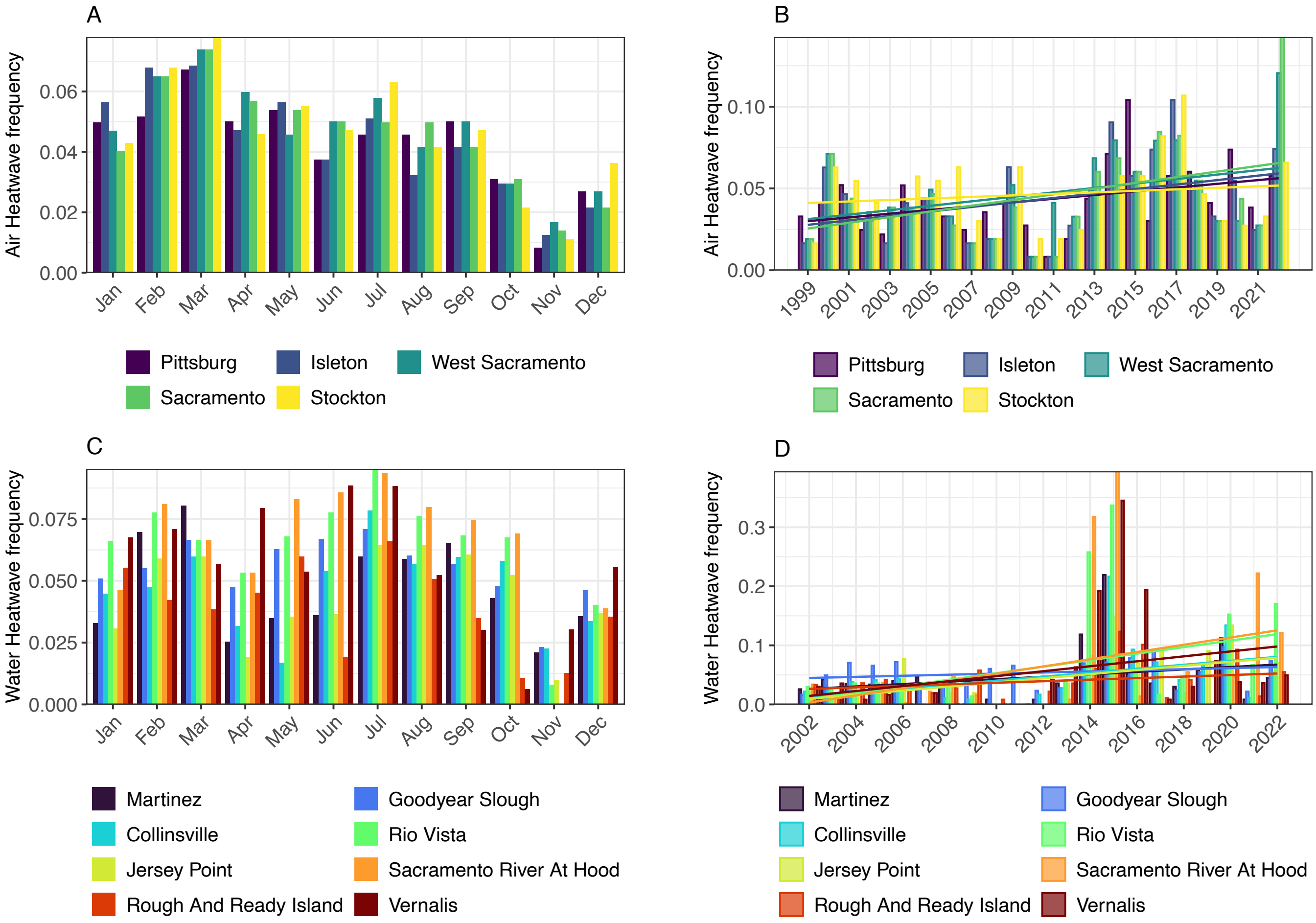

Figure 4 Frequency of air (**A** and **B**) and water (**C** and **D**) heatwave days by month (**A** and **C**) or year (**B** and **D**). Trendlines are linear models across year for each station or city. The best model fit to the full air or water dataset found significant ($p < 0.05$) increases in the frequency of heatwave days for both air and water temperatures. Locations are ordered from West to East. Heatwaves are defined as 3 or more contiguous days that exceeded the 90th quantile. The 90th quantiles for each location are defined in Figure 3.

undoubtedly affect species interactions, shift communities, and reshape ecosystem dynamics.

Although understanding commonalities among taxa is useful for understanding broader effects, the various taxonomic groups that make up the Delta ecosystem each have unique aspects to consider, and each will play a distinct role in a warmer Delta. In our literature review below, we focus largely on the aquatic species of the Delta because they are well-studied, and water plays a central role in this system. Note that we also focus specifically on ecological effects of warming and extreme heat events. For a general overview of the various effects associated with climate change (e.g., sea level rise, increased frequency of flood and drought years, etc.) for the aquatic ecosystems found in the upper estuary, see the synthesis report produced by the Interagency Ecological Program (Climate Change MAST 2022).

Aquatic Taxa

Phytoplankton

In the estuary, the phytoplankton community primarily comprises the phyla Cyanophyta (cyanobacteria), Bacillariophyta (diatoms), Dinoflagellata (dinoflagellates), Chrysophyta (chrysophytes), Cryptophyta (cryptophytes), and Chlorophyta (green algae). Among these

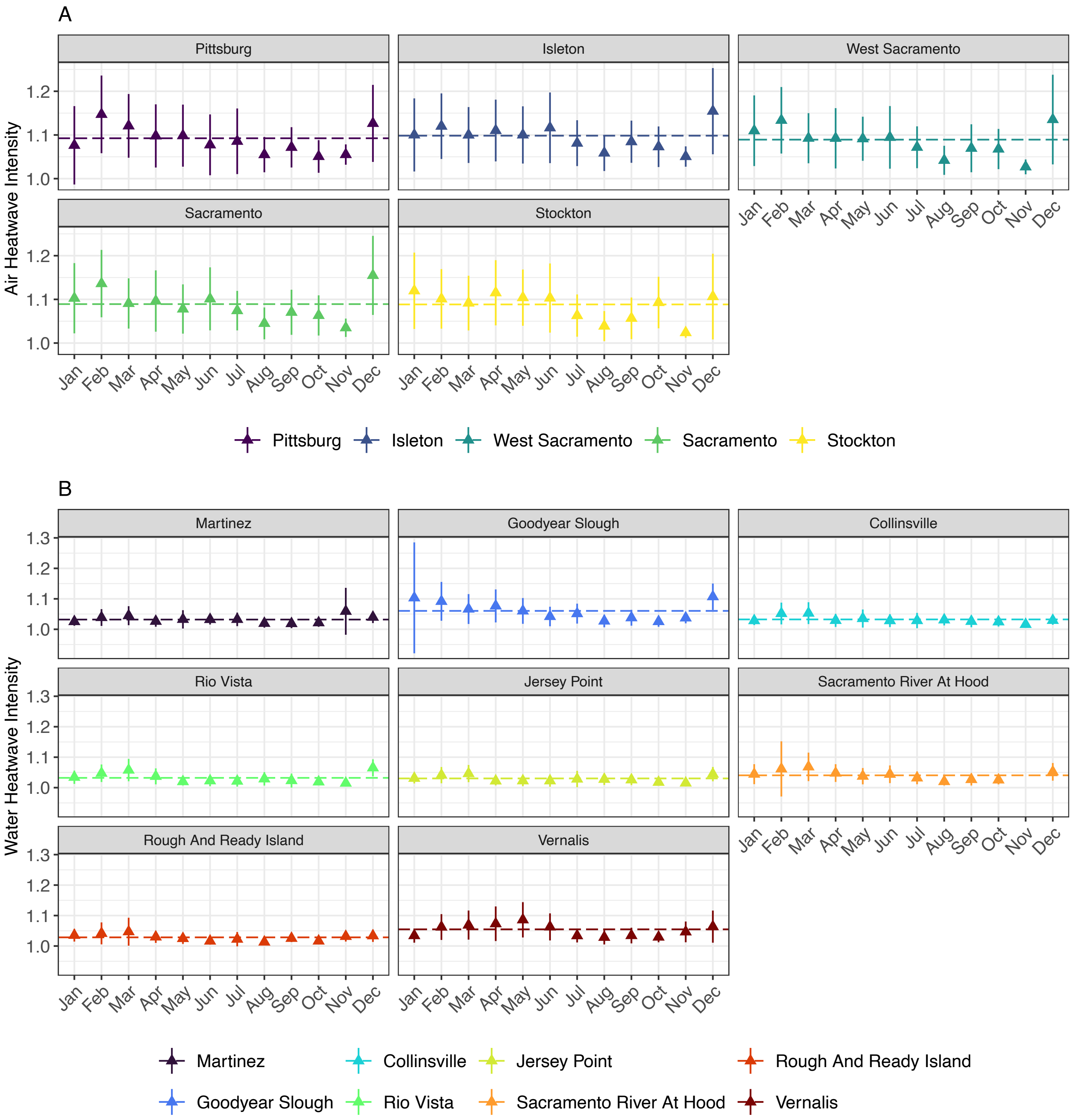

Figure 5 Air and water heatwave intensity by month. *Dashed line* indicates mean intensity for each city or station. *Points* and *bars* indicate mean and standard deviation of intensity. Locations are ordered from West to East. Heatwaves are defined as 3 or more contiguous days that exceeded the 90th quantile. The 90th quantiles for each location are defined in Figure 3.

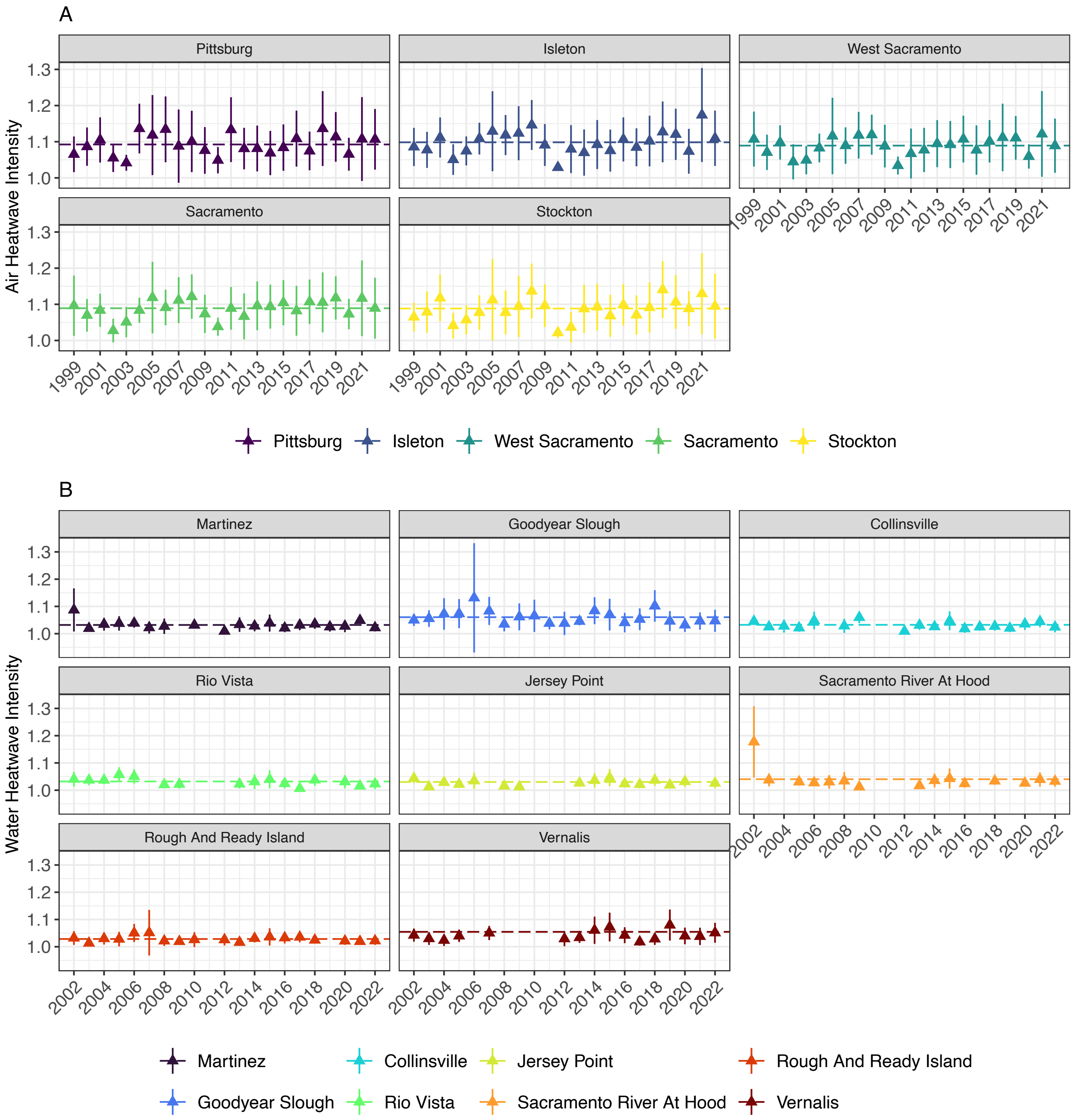

Figure 6 Air and water heatwave intensity by year. *Dashed line* indicates mean intensity for each city or station. *Points* and *bars* indicate mean and standard deviation of intensity. Years with no *points* did not have heatwaves. Locations are ordered from West to East. Heatwaves are defined as 3 or more contiguous days that exceeded the 90th quantile. The 90th quantiles for each location are defined in Figure 3.

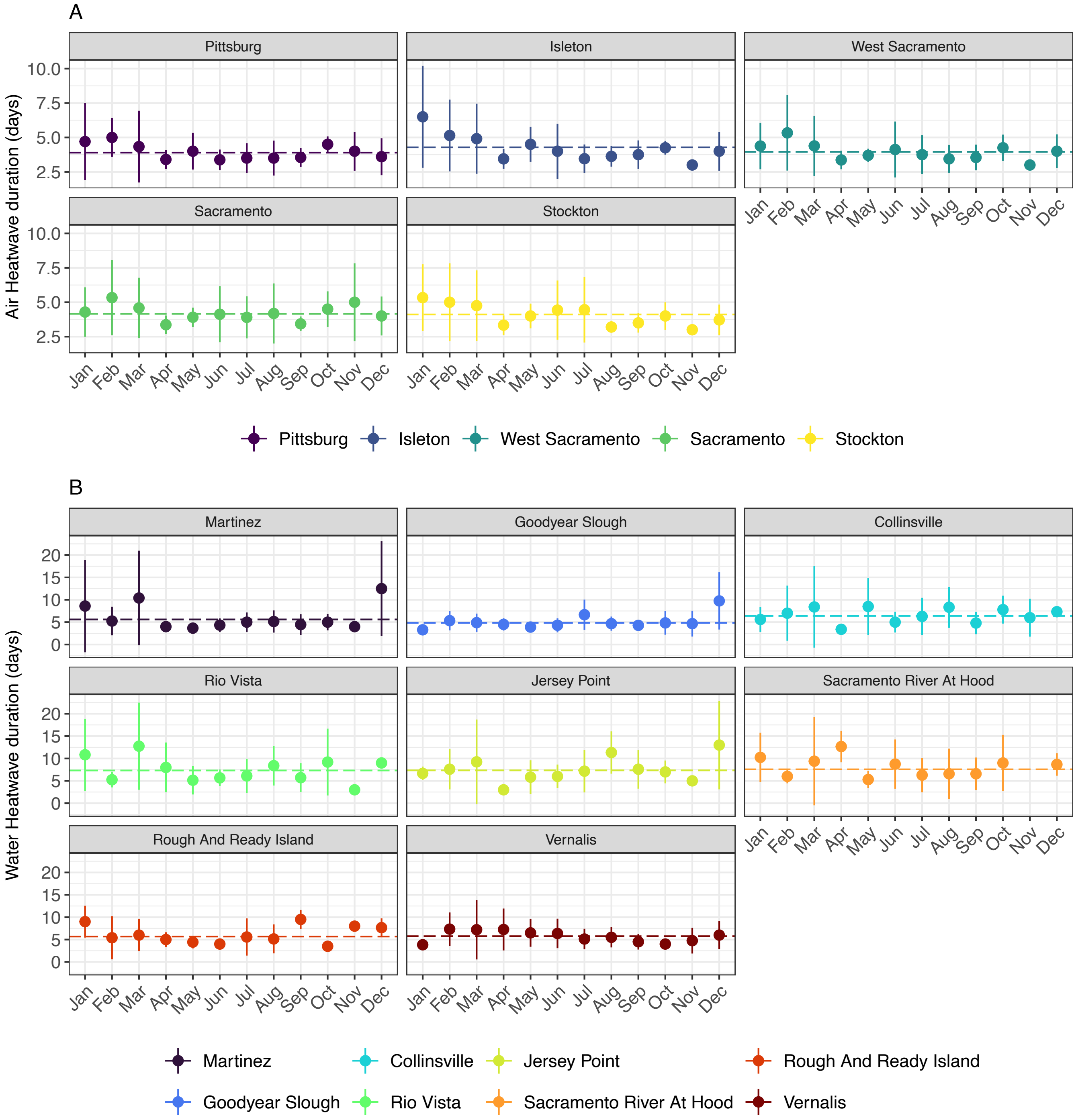

Figure 7 Air and water heatwave duration by month. *Dashed line* indicates mean intensity for each city or station. *Points* and *bars* indicate mean and standard deviation of intensity by month. Years with no *points* did not have heatwaves. Locations are ordered from West to East. Heatwaves are defined as 3 or more contiguous days that exceeded the 90th quantile. The 90th quantiles for each location are defined in Figure 3.

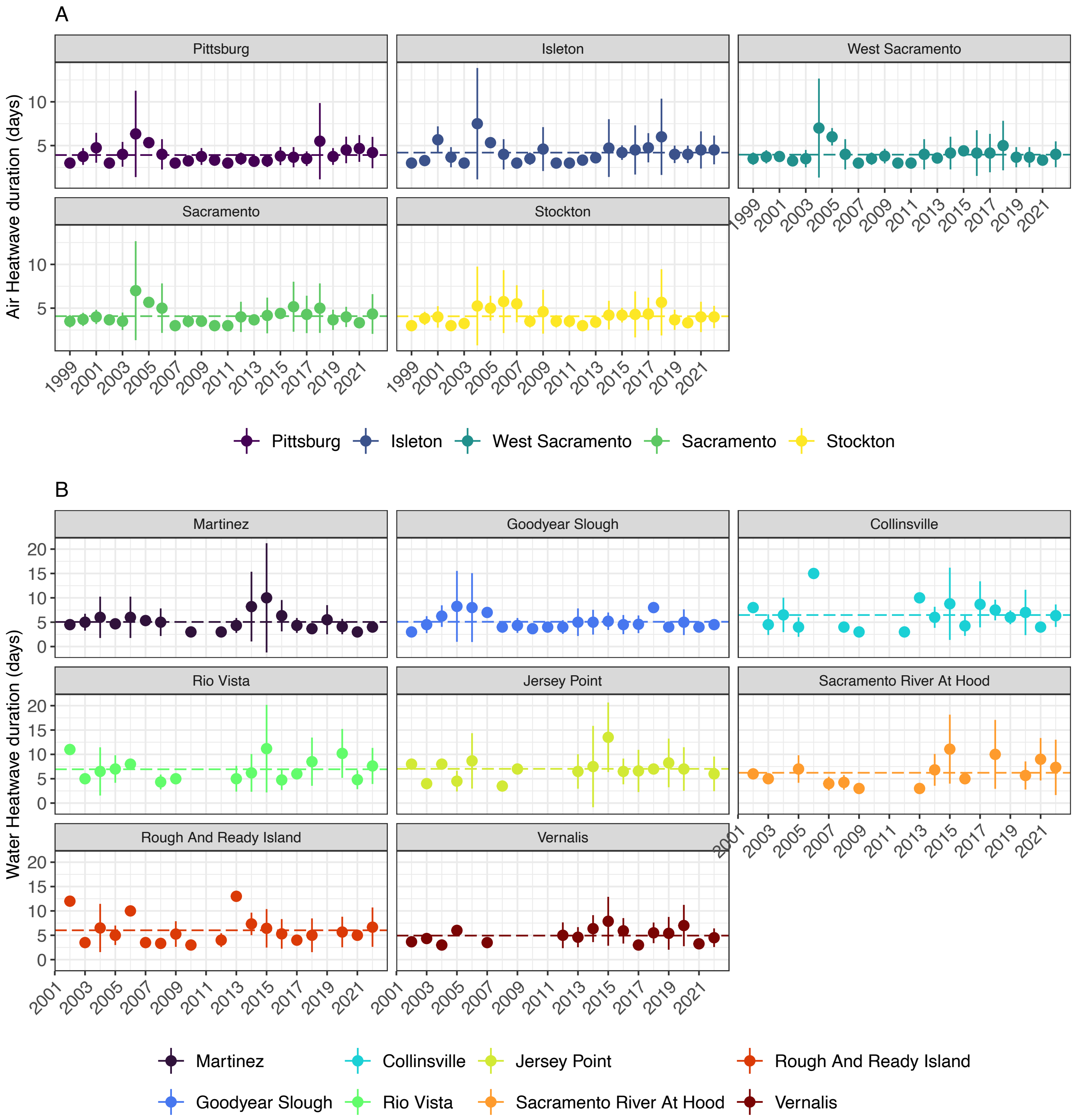

Figure 8 Air and water heatwave duration by year. *Dashed line* indicates mean intensity for each city or station. *Points* and *bars* indicate mean and standard deviation of intensity by month. Years with no *points* did not have heatwaves. Locations are ordered from West to East. Heatwaves are defined as 3 or more contiguous days that exceeded the 90th quantile. The 90th quantiles for each location are defined in Figure 3.

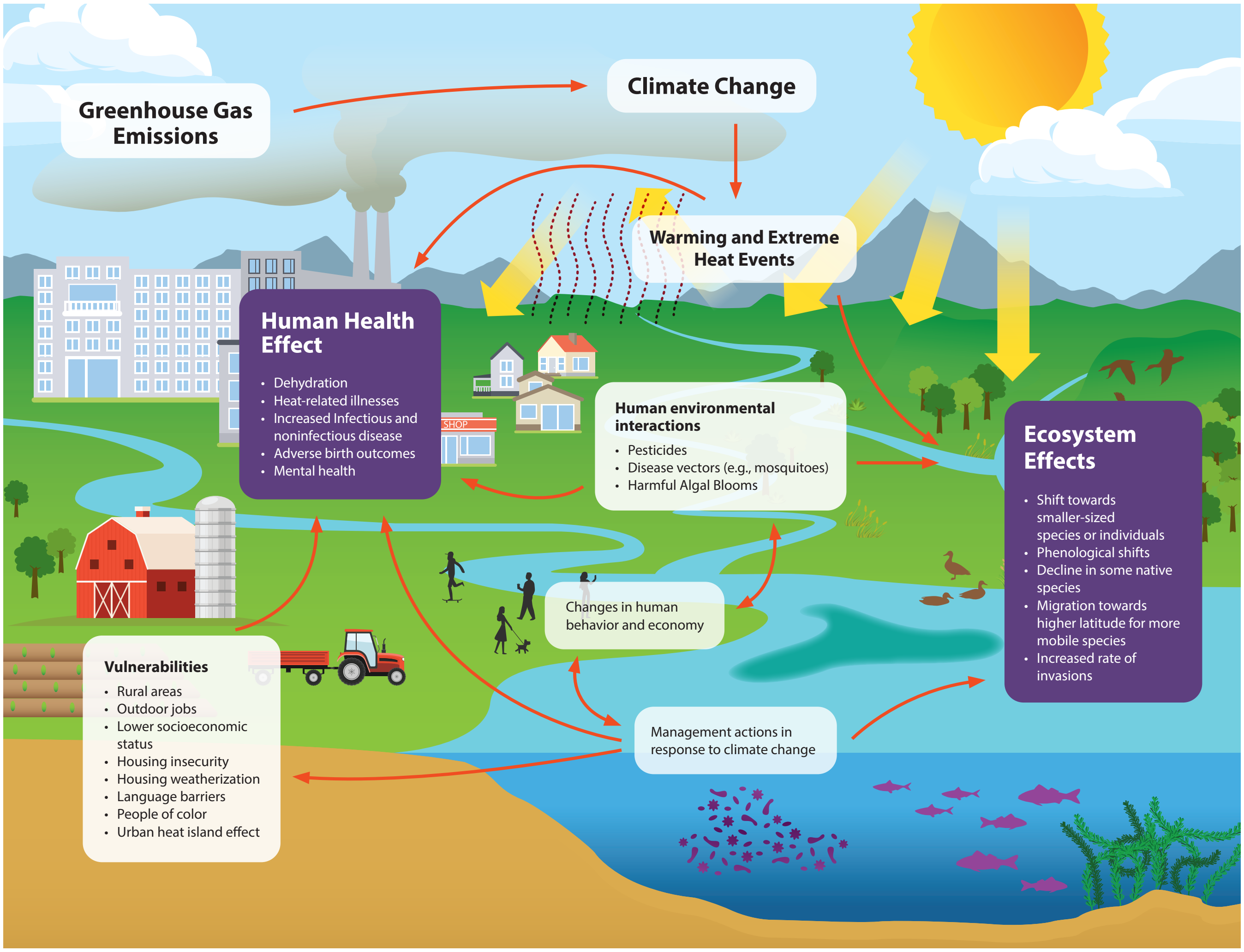

Figure 9 Conceptual model of primary effects of climate change-driven high temperatures and extreme heat events to the ecosystem and humans within the upper San Francisco Estuary. Credit: Illustration by Vincent Pascual with the California Office of State Publishing.

taxa, the harmful algal blooms (HABs) of the cyanobacterium *Microcystis* in freshwater regions have garnered a lot attention since its first detection in 1999, as a result of their negative health effects on fish species, humans, and pets (Lehman et al. 2010; Acuña et al. 2012; Kudela et al. 2023).

While overall phytoplankton biomass indexed by chlorophyll-*a* is a coarse metric of primary productivity irrespective of fish and wildlife benefits (e.g., high chlorophyll-*a* can indicate a HAB or a beneficial algal bloom), it is a useful metric for broad productivity. In the estuary, chlorophyll-*a* appears to be more closely linked to flow or residence time rather than temperature, where low flow conditions (and thus higher residence times) lead to higher chlorophyll-*a* levels (Conomos et al. 1979; Cloern et al. 1985; Lehman 1996; Jassby 2008). Nevertheless, phytoplankton biomass will be affected by warmer temperatures and increased heatwave frequency. Since 1972, the timing of phytoplankton blooms in the estuary has shifted earlier in the year, possibly, in part, as a result of warmer conditions (Merz et al. 2016). Higher water temperature can lead to either net increases or decreases in overall biomass, depending on the taxa present, their bioenergetics, other environmental conditions (e.g., depth, salinity, nutrient availability, etc.), and food-web interactions. Warmer conditions may lead to increased growth and biomass, but can also increase respiration, which can, in turn, reduce biomass. This was illustrated in field studies in the Yolo Bypass, where both high growth and respiration rates at high water temperature led to net negative growth (Lehman et al. 2008). In the Sacramento and San Joaquin rivers, chlorophyll-*a* levels are associated with higher water temperatures (Lehman 1992). However, in Suisun Bay, this relationship seems to be reversed (i.e., negative correlation between chlorophyll-*a* and water temperature), possibly because larger marine species drive chlorophyll-*a* concentrations and they are associated with cooler tidal waters (Lehman 1992). Consumers of phytoplankton such as clams and zooplankton can suppress phytoplankton biomass (Thompson et al. 2008; Kimmerer and Thompson 2014), and thus, warmer temperatures may lead to lower phytoplankton availability because metabolic and consumption rates by these primary consumers increase with higher temperatures.

The estuary's phytoplankton community composition and structure can also be altered by the rising temperatures and increasing heatwaves. Generally, cyanobacteria exhibit optimal growth at higher temperatures than dinoflagellates and diatoms (Paerl et al. 2011; Griffith and Gobler 2020). As such, elevated water temperature in the estuary appears to favor some green algae and cyanobacteria, particularly the toxic cyanobacteria *Microcystis, Dolichospermum,* and *Aphanizomenon* (Lehman et al. 2017; Lehman et al. 2021). Globally, the warming effects of climate change are expected to increase the frequency and intensity of HABs associated with cyanobacteria (Paerl and Huisman 2008; Harke et al. 2016; Burford et al. 2020; Griffith and-Gobler 2020). More frequent heatwaves in the summer, as we observed for water temperature, may further contribute to increases in HABs. As water temperature becomes warmer (>20 °C) and abundance of cyanobacteria increases, other species may also be negatively affected by allelopathy (Lehman et al. 2021). This allelopathy may be partially driving the observed negative correlation between the abundance of *Microcystis* and the abundance of diatoms and green algae in the system (Lehman et al. 2010; Lehman et al. 2013; Lehman et al. 2017). Although diatoms generally prefer lower water temperatures relative to cyanobacteria (Paerl et al. 2011; Glibert et al. 2014; Griffith and Gobler 2020), the effect of elevated water temperature depends on the region and particular taxa. Between 1975 and 1993, water temperature was negatively correlated with diatom carbon in the Delta, but this relationship is reversed in Suisun Bay (Lehman 2004). Elevated water temperature is associated with increased abundance of certain centric diatoms such as *Aulacoseira granulata* and *Skeletonema potamos,* but a decrease in the abundance of pennate diatoms, including *Asterionella,* and *Nitzschia* (Lehman 2000). However, pennate diatoms, green algae, and cryptophytes can also increase with higher water temperature during drought years (Lehman and Smith 1991; Lehman 2000; Lehman 2007). Another potential effect to highlight as the estuary warms is that phytoplankton species composition may shift away from large diatoms towards smaller pico- or nano-plankton with lower nutritional quality (Hare et al. 2007; Marañón et al. 2012; Cloern 2018). Overall, these disparate effects on the various phytoplankton taxa could shift the quality of phytoplankton food for zooplankton, with cascading effects to higher trophic levels such as fishes (Cloern 2018).

Clams

Two invasive bivalves have had an outsized effect on the estuary's food web, severely grazing down the standing stock of phytoplankton biomass: *Potamocorbula amurensis* and *Corbicula fluminea*. Since its introduction in 1986, the overbite clam *P. amurensis* has become a constant in the brackish region of the estuary around Suisun Bay. *P. amurensis* possesses extremely high grazing and reproductive rates, and its establishment led to a long-term decrease in chlorophyll-*a* levels within Suisun Bay since the mid-1980s (Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer 2004; Dugdale et al. 2016; Lucas et al. 2016). *P. amurensis* can even directly consume zooplankton (Kimmerer et al. 1994) and has been suggested as one of the drivers for the pelagic organism decline in the estuary (Kimmerer 2006; Thomson et al. 2010). Another introduced bivalve is the Asian clam *C. fluminea*, a species that is more common in the freshwater parts of the estuary (e.g., the Delta). *C. fluminea* were introduced in the 1940s, and although they can affect pelagic productivity, their grazing rates are four times lower than *P. amurensis* (Kimmerer et al. 2019). As such, while *C. fluminea* abundance has been linked to lower productivity in local areas within the Delta (Lopez et al. 2006), their overall effect on the system is likely lower than *P. amurensis*.

Both *P. amurensis* and *C. fluminea* tolerate high temperatures and may benefit from the rising temperatures. To date, there has been no indication that the temperature range observed in the estuary (roughly 5 to 29 °C; see Mahardja et al. 2022) would limit distribution or reproduction of *P. amurensis* (Miller and Stillman 2013). Although information on the optimum thermal range for *P. amurensis* is limited, *P. amurensis* is considered a eurythermal species that can tolerate a broad range of temperatures (Kamenev and Nekrasov 2012). A congener of *P. amurensis* was found to have the greatest growth rates between 22 and 28 °C, with reproduction occurring at a lower range between 12 and 23 °C (Carlton et al. 1990). Meanwhile, *C. fluminea* may be able to tolerate water as cold as 0 °C (Müller and Baur 2011), with a lethal upper limit of 38 °C (Nascimento et al. 1996), and optimal range around 18–25 °C (Xiao et al. 2014). Assuming no food limitation or density dependence, higher overall temperatures will likely have no negative impacts and may even benefit both *P. amurensis* and *C. fluminea* because water temperatures would be within their optimal range for longer throughout the year. Filtration rates for both species are expected to increase with temperature up to a certain point, though this relationship has not yet been experimentally tested in *P. amurensis* and may be dampened by temperature stratification in some deeper waters (Mahardja et al. 2022). Increased filtration rates may have a larger effect in shallow water where these bivalves can more effectively filter the entire water column (Thompson et al. 2008). Warmer conditions throughout the year may also mean that the reproductive period of *P. amurensis* would begin and end earlier each season. Considering both species' affinity to warm temperatures, it seems unlikely that extreme heat events will cause considerable harm to their populations in the estuary. However, the combination of high temperature and low flows can potentially lead to low dissolved oxygen levels, which can, in turn, reduce the growth rates of these species and even cause large-scale die-offs (Cherry et al. 2005; Ilarri et al. 2011). Thus, the patterns we detected of increasing heatwave frequency and greater heatwave frequency in the winter and summer may benefit *P. amurensis* and *C. fluminea*, unless it results in low dissolved oxygen levels.

Aquatic Plants

In the past 2 decades, invasive aquatic plants have increased their extent in the Delta and acted as eco-engineers degrading the ecosystem (Hestir et al. 2016; Khanna et al. 2018). As they increase in extent, they expand their niche through positive feedbacks (Lacy et al. 2021). More than 75% of submerged aquatic macrophytes cover in the Delta are non-native, while more than 90% of floating aquatic plant cover is non-native (Christman et al. 2023). Hence, it is critical to know how climate change will affect invasive species distribution in the Delta.

Most submerged and floating invasive species have their optimal growth somewhere between 10 to 30°C. Above 30 °C, growth slows down for most species in the Delta (Hartleb et al. 1993; Madsen and Smith 1997; Malik 2007; Wilson et al. 2007; Thouvenot et al. 2013; Borgnis and Boyer 2016). In the 2014–2016 drought, air temperatures in the Delta region were higher than 30 °C for a third of the year (~120 days; Figure 4), but it was even hotter in 2020 when the Sacramento and Stockton areas both recorded more than 140 days above 30 °C. Highs of 30 °C can be observed as early as March–April and late into October in the Delta. Thus, higher temperatures likely reduce cover of invasive aquatic plants in peak summer months, and will continue to affect growth with more frequent heatwaves that result from climate change. However, on an interannual scale, there might not be much difference in biomass due to warmer temperatures in spring and fall that would lead to a longer growing season. For example, during the 2014–2016 drought and in 2022, there were heatwaves during winter and spring which likely prolonged the growth season (Figure 4).

While most of this article focuses on warm temperatures and extreme heat events, opposite extremes and cold temperatures may significantly limit invasive aquatic plant growth and survival. For example, many of the invasives currently found in the Delta have limitations at the lower end of the temperature scale. Most species have much slower growth at 10 °C and below (Hartleb et al. 1993; Madsen and Smith 1997; Shen et al. 2005; Wilson et al. 2007). Two commonly found invasive species in the Delta, water hyacinth (*Eichhornia crassipes*) and watermilfoil (*Myriophyllum spicatum*), are both sensitive to frost, which can kill off all biomass. However, their overwintering organs can survive for a few days in below-zero temperatures (Penfound and Earle 1948; Aiken et al. 1979; DiTomaso et al. 2003). Several consecutive days of frost can be more permanently damaging to the distribution of these species. Seeds can also be vulnerable at very high (Salter et al. 2010) or very low temperatures (Hartleb et al. 1993); however, some of the principal invasive species in the Delta propagate primarily through vegetative reproduction or storage organs rather than through seeds. We observed that heatwaves were more common in the winter for both air and water temperature. This may have facilitated the invasion and spread of invasive aquatic vegetation by reducing exposure to cold temperatures.

It is worth noting that the Delta currently hosts species that are highly heat-tolerant. Alligator weed *Alternanthera philoxeroides* shows robust growth at least up to 32 °C (Julien et al. 1995). There are no studies we could find on ideal temperature windows for Ribbon weed *Vallisneria australis*, but *V. americana*—a species very close in phylogeny to *V. australis* (Les et al. 2008) but not present in the Delta—was reported to have robust growth up to 38 °C (Bartleson et al. 2014), which is higher than all invasive aquatic plants currently found in the Delta. If *V. australis* has a similar tolerance to high temperatures, it is likely that this species may have a competitive advantage over other macrophytes as extremely high temperatures become more common.

Zooplankton

Zooplankton are heterotrophic plankton composed of detritivores (feed on detrital organic matter such as degraded plant matter), primary consumers (feed on phytoplankton), and secondary consumers (feed on other zooplankton). In the estuary, there is high interest in the status of the zooplankton community because they are the dominant prey item for listed pelagic fish species such as Delta Smelt (*Hypomesus transpacificus*) and Longfin Smelt (*Spirinchus thaleichthys*), and the decline of these pelagic fish species has been partially attributed to the system's decline in the availability and quality of zooplankton (Kimmerer 2006; Kratina and Winder 2015; Kimmerer and Rose 2018). Currently, the bulk of zooplankton biomass comprises calanoid and cyclopoid copepods. However, cladocerans can be abundant (by biomass) in freshwater regions, and rotifers can be abundant between December through April (Bashevkin, Hartman, et al. 2022). Mysid shrimp species were once dominant but have declined greatly over the past 40 years (Winder and Jassby 2011). Similar to other taxa, the estuary's current zooplankton community has also been shaped by a number of species invasions. Native zooplankton species that were once primary prey items for native fishes have been largely replaced by invaders that originated from East Asia (Winder and Jassby 2011). Some of these introduced species have become critical food source for native fishes (e.g., *Pseudodiaptomus forbesi*), while others contribute little to fish diets and may even suppress key prey species for fishes (e.g., *Limnoithona tetraspina*) (Slater and Baxter 2014; Kayfetz and Kimmerer 2017).

Hydrology and the salinity field are the primary driving forces for zooplankton abundance and distribution in the estuary (Kimmerer 2004). Nevertheless, zooplankton can be particularly sensitive to warming and extreme heat events because of their short generation times and high physiological sensitivity to temperature (Richardson 2008). Higher temperature will lead to an increase in growth rate (when food is not limiting), decreased body size, and potentially changes to phenology and community structure. Studies in other systems indicate that warmer temperatures result in shifts toward lower body size within a species, or toward species with smaller sizes overall (Garzke et al. 2015; Rice et al. 2015). Discrete extreme heatwave events can also cause a notable change in zooplankton community composition from larger to smaller taxa accompanied by a decline in biomass, as observed in Western Australia (Richardson et al. 2020). These changes may have already taken place in the estuary, as the small cyclopoid copepod *Limnoithona tetraspina* has dominated over the larger calanoid copepods in the past decade (Bouley and Kimmerer 2006). Furthermore, the smaller mysid *Hyperacanthomysis longirostris* currently dominates over the larger *Neomysis mercedis* (Avila and Hartman 2020). One change potentially attributable to temperature that has already been observed in the estuary is that peak abundance timing of various zooplankton taxa has shifted earlier in the past 40 years (Merz et al. 2016). Although these changes have not been directly linked to warmer temperatures, this trend is consistent with expectations of earlier phenology with warming temperatures (Richardson 2008), and likely to continue with warmer spring temperatures, potentially earlier spring run-off, and increasing heatwave frequency. The relatively high frequency of heatwaves in the winter that we observed may have already contributed to these shifts in timing. The decoupling of timing between phytoplankton and zooplankton blooms has led to reduced zooplankton availability in another system (Winder and Schindler 2004), and altered zooplankton phenology can lead to trophic mismatch wherein zooplankton prey are unavailable during critical feeding periods for larval fishes (Durant et al. 2007). Such trophic mismatches may have negative repercussions for fish species of conservation interest within the estuary.

Fishes

Compared to free-floating aquatic taxa and terrestrial taxa, the increased mobility of fishes provides an advantage to combat increasing water temperatures and extreme events projected with climate change. Short-term, fishes can rapidly move to more suitable thermal habitat (i.e., refugia) to behaviorally regulate their body temperature or increase food consumption (or both) to meet enhanced energy demands. Long-term, fishes may shift their distributions or life-history strategies (i.e., migration timing) to habitats that favor growth, reproduction and/or avoid unsuitable conditions. However, the Delta ecosystem of today may already be limiting short or long-term movement responses for native species. For example, summer–fall water temperatures already frequently exceed fish species thresholds (Pien et al. 2024) and we found higher heatwave frequency in the summer, thermal refugia in deeper water is limited (Mahardja et al. 2022), and habitat may be constrained by other physical or biotic factors such as salinity and turbidity, food availability, and predation. Anadromous fishes in the Delta could seek temperature refuge at higher latitudes or in more brackish waters but their ability to move may be limited by salinity tolerance. Sustained warmwater habitat and extreme heat events in the Delta will likely affect fish populations differently, based on the species' capacity to cope with high temperatures, their life-history strategy, their role in the food web, and how they are managed in the system.

The ability of fish species to survive extreme heat events depends on their capability to withstand temperature stressors (i.e., frequency, intensity, and duration), which may be limited for several native Delta species with lower temperature thresholds (Pien et al. 2024). Fishes are ectothermic, meaning their body temperature mimics their environmental temperature; as water temperature increases, it directly affects their physiological performance, behavior, and survival. Fishes cope with temperature challenges by avoiding it (i.e., moving), adjusting their physiology and biochemistry (i.e., acclimation and acclimatization) to withstand the challenge and maintain performance, or adapting to long-term temperature changes over generations. The duration and energy required for physiological adjustments—e.g., changes in cardio-respiratory performance (Farrell et al. 2009), hormone regulation and energy mobilization (Bonga 1997), heat response mechanisms (Iwama et al. 1999)—to cope with temperature challenges will likely increase alongside the increased duration of heat events in the estuary (Figure 6B and Figure 7B). Sensitivity to warming and extreme heat events, however, can vary among and even within species as a result of physiology, life history, and other interacting stressors. Depending on the fish species, region, and other environmental factors, temperature stress can result in various changes from an individual level, and influence phenology to population and ecosystem level effects (Petitjean et al. 2019).

Native fishes in the Delta are likely more vulnerable to temperature extremes compared to non-native species, given that a number of native species are associated with cold water (< 22 °C) (Moyle et al. 2013; Brown et al. 2016; Jeffries et al. 2016). Meanwhile, non-native fish species in the Delta are often characterized as "generalist" species because they can typically tolerate wide ranges of environmental parameters, including water temperature. For example, two of the most abundant non-native fish species in the Delta—Mississippi Silverside (*Menidia audens*) and Largemouth Bass (*Micropterus salmoides*)—seem to prefer warm water and possess high temperature tolerances (Mahardja et al. 2016; Davis, Cocherell, et al. 2019). In contrast, some native fish species are more "specialized," with relatively narrow ranges of habitat conditions they can tolerate, reflecting the ecological regime to which they have adapted. For example, the listed native osmerids (Longfin Smelt and Delta Smelt) and salmonids that use the Delta are more cold-adapted, with lower temperature ranges for optimal physiological performance and tolerances (Moyle et al. 2013; Pien et al. 2024), and some may even require lower temperatures for reproduction and optimal growth than what current Delta conditions provide (Lewis et al. 2021). Nevertheless, it is worth noting that there are native fish species—such as Sacramento Blackfish (*Orthodon microlepidotus*) and Splittail (*Pogonichthys macrolepidotus*)—that can tolerate relatively high temperatures (> 30 °C) (Young and Cech 1996; Moyle 2002; Moyle et al. 2004), potentially making them more resilient in the face of climate change (Mahardja et al. 2021).

Studies have shown for ectotherms such as fishes, warmer temperatures should also lead to reduced body size (Gardner et al. 2011). Although this has not yet been evaluated for this estuary's fishes, evidence from other systems is mounting (Oke et al. 2020; Ikpewe et al. 2021), and it may only be a matter of time before we observe this shift in the estuary's fish assemblage. With rising temperatures, we also expect more frequent invasions of new fish species into the Delta. A rapid establishment of a new fish species (Bluefin Killifish *Lucania goodei*) in the Delta occurred just a few years ago, likely stemming from an improper release of aquarium fish (Mahardja et al. 2020). Cold winter temperatures are generally thought to be a barrier that would prevent many fish species in the aquarium trade from becoming established in the upper estuary (Chang et al. 2009). Warmer winters and more frequent heatwaves in the colder months will increase the likelihood of successful introductions of new species into the estuary.

Fishes may also be affected by extreme temperatures and heat events through altered ecological interactions. For example, the effects of increased temperature and heat events on the food web, competition, parasitism, and disease may exacerbate climate-change effects on native fishes. Warmer conditions may confer physiological and behavioral advantages on piscivorous fishes as a result of reductions in prey-avoidance capacity for native prey species and enhanced predator activity (Davis, Hanson, et al. 2019; Nobriga et al. 2021; McInturf et al. 2022). Field surveys suggest that as water temperature reaches 20 °C, juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) may experience high predation mortality due to a mix of reduced swimming capacity for juvenile Chinook Salmon and increased predation rate by the non-native Striped Bass (*Morone saxatilis*) and Largemouth Bass (Nobriga et al. 2021), two piscivorous species with relatively high temperature tolerances (Lapointe et al. 2014; Davis, Cocherell, et al. 2019). Recent laboratory studies that investigated the effect of warming on juvenile Chinook Salmon, Delta Smelt (*Hypomesus transpacificus*), and Largemouth Bass interactions demonstrated that thermal biology and swimming speeds of both prey (Davis, Cocherell, et al. 2019; McInturf et al. 2022) and predators get faster with warmer temperatures. However, prey species demonstrate thermal constraints in other swimming mechanisms at warmer temperatures such as reduced group cohesion in shoals (Delta Smelt) and reduced number of bursts and burst speeds (Chinook Salmon) that likely limit their ability to avoid predation, especially with increased consumption rates by more thermally adapted predators such as Largemouth Bass (Davis, Hanson, et al. 2019; McInturf et al. 2022). Changes at the lower trophic levels of the food web from elevated temperatures and extreme heat events as summarized in previous sections (e.g., shift toward smaller-sized zooplankton species, potential proliferation of cyanobacteria, etc.) may also lead to major consequences to the fish assemblage of the upper estuary. It is important to consider these indirect effects of extreme temperatures on fish species, as they may manifest unexpectedly, with significant repercussions for conservation efforts.

Understanding the temperature vulnerability of native Delta fishes' and their capacity to adapt to increasing heat extremes are of particular concern to Bay–Delta resource managers given that many native fish species are declining, an increasing number are listed as threatened or endangered under the federal and California ESAs, and regulations to protect them affect water operations. Osmerids and salmonids are relatively sensitive to warm temperatures, with limited capacity to survive the projected thermal landscape of the Delta without large-scale management intervention. Already, summer temperatures and heatwaves have demonstrated deleterious effects to some native fishes, and the upper estuary is becoming increasingly thermally unsuitable in the long term for Delta Smelt, a native osmerid species that are year-round residents in the estuary (Brown et al. 2013; Brown et al. 2016; Lewis et al. 2021; Pien et al. 2024). Below, we highlight the temperature sensitivity and adaptability for a few key fish species of management concern that use the Delta for at least part of their life cycle.

Delta Smelt. The native Delta Smelt is a small pelagic fish in the estuary that lives 1 to 2 years, is semi-anadromous, and has a relatively specific zooplankton diet and low reproductive capacity compared to other species. Their once-abundant population has declined rapidly over the years, especially after the pelagic fish community collapse in the early 2000s (Sommer et al. 2007; Mac Nally et al. 2010), and the species is currently listed under both the federal (USFWS 2019) and California ESAs (CNDDB 2023). Delta Smelt occupy mostly tidal areas including littoral, channel, marsh, and bay habitats with varied brackish and freshwater conditions, and moderate temperatures ranging from 7 to 25 °C (Sommer and Mejia 2013). Their distribution varies by life-stage and season; during springtime, adult fish spawn in freshwater; in late spring and summer, larvae and early juveniles migrate downstream to rear until winter flows increase, when they migrate back upstream to spawn (Moyle et al. 2016). The downstream western distribution of Delta Smelt extends to San Pablo Bay and Suisun Bay where they experience cooler temperatures with more seawater influence and higher turbidities, while their upstream eastern distribution in the Sacramento River and San Joaquin River can experience warmer and increasingly unsuitable (> 22 °C) conditions, particularly in later summer–fall months (Bashevkin, Mahardja, et al. 2022; Mahardja et al. 2022; Smith and Nobriga 2023; Pien et al. 2024).

Field and laboratory studies suggest Delta Smelt are sensitive to water temperatures > 22 °C, likely from a combination of physiological, behavioral, and interspecific interactions. With acclimation, Delta Smelt can tolerate water temperatures of 25 to 30 °C before mortality occurs (Swanson et al. 2000; Komoroske et al. 2014; Davis, Hansen, et al. 2019); however, long-term field surveys demonstrate that Delta Smelt occurrence in the Delta is greatest near 20 °C (Sommer and Mejia 2013), with a majority of adults and juveniles caught at water temperatures < 22 °C (Bennett 2005; Nobriga et al. 2008). Field detections of sub-lethal temperature thresholds around 20 to 23°C (Davis et al. 2022) are consistent with studies that link these temperatures to lower growth (Lewis et al. 2021), molecular stress (Komoroske et al. 2015; Jeffries et al. 2016; Komoroske et al. 2021), consumption limitations (Smith and Nobriga 2023), and altered behavior than could result in elevated energy demands and predation (Davis, Hansen, et al. 2019).

The temperature sensitivity of Delta Smelt and the species' limited capacity to adapt to future temperature increases will undoubtedly challenge the species' persistence in the Delta. Increased frequency of summer heatwaves, particularly in drought periods (Figure 4), will continue to constrain the population, given their annual lifespan. The highest water temperatures and heat events are occurring at the juvenile to sub-adult life stage, when Delta Smelt should be actively foraging and growing to reproductive size for migration and spawning the following year. Warmer conditions and extreme heat events will increase the energy requirements of Delta Smelt (physiological and swimming activity) that must be met by energy and food supply to maintain growth and/or find suitable habitat; however, foraging and consumption may be thermally constrained (Smith and Nobriga 2023), and the extent of thermally suitable habitat in the estuary is shrinking (Halverson et al. 2022). Food availability and quality for Delta Smelt has been suppressed through multiple introductions of invasive species (Kimmerer et al. 1994; Winder and Jassby 2011; Kayfetz and Kimmerer 2017), which may exacerbate the extreme temperature effects—potentially resulting in mortality if not stunted growth, delayed maturity, decreased fecundity, and lower spawning success for the next cohort (Rose et al. 2013; Damon et al. 2016). For example, spawning of Delta Smelt is most common between 9 to 18 °C, with a 20-°C upper limit (Bennett 2005; Damon et al. 2016). Increased temperature or extreme heat events in springtime during spawning season may limit reproductive success by truncating the spawning season (Brown et al. 2016). Indeed, in drought years that are associated with warmer springtime water temperature (Bashevkin and Mahardja 2022), adult Delta Smelt display smaller clutch sizes and eggs (Kurobe et al. 2022). Yet some hope remains, as Delta Smelt have demonstrated some plasticity in response to changing temperature conditions. Otolith data indicate that the species' spawning period shifts earlier with warmer temperatures (Lewis et al. 2023). Delta Smelt have also been observed using alternate spawning and rearing habitat correlated with earlier spawning times (Mahardja et al. 2019). However, shifts in phenology or spawning habitat may create misalignment with normal trophic dynamics (e.g., prey availability).

As the Delta Smelt population has become more reliant on supplementation of cultured fish in recent years, there is a need to better evaluate the capacity of cultured Delta Smelt to cope with extreme field temperatures and how it can be ameliorated (e.g., with higher food availability). This is imperative given the domestication level of cultured Delta Smelt (Finger et al. 2018; Ellison et al. 2023) and their likely local adaptations to more stable and cooler hatchery conditions. Recent studies that demonstrated high survival rates of cultured Delta Smelt in semi-natural environment provide some optimism that cultured Delta Smelt can handle the estuary's highly dynamic conditions (Hung et al. 2019; Baerwald et al. 2023). However, heatwaves may be lethal if they are unable to find suitable thermal habitat as demonstrated in a large mortality event in an enclosure experiment in 2019 within the North Delta region (B. Davis, pers. observation). The high summer heatwave frequency we observed for water temperatures makes this especially challenging.

Longfin Smelt. The native Longfin Smelt (*Spirinchus thaleichthys*) is a small pelagic, schooling, anadromous fish in the estuary that lives for 2 to 3 years. Longfin Smelt were historically one of—if not *the* most—abundant fish in the estuary, but were state listed as threatened in 2009 and federally listed as endangered in 2024 (USFWS 2024) as their population has decreased to less than 1% of what was observed in the 1980s (Hobbs et al. 2017). The distribution of Longfin Smelt extends as far north as the Aleutian Islands in Alaska; however, the estuary's Longfin Smelt has been shown to be a genetically distinct population (Sağlam et al. 2021). Longfin Smelt occupy tidal and open-water areas including littoral, channel, marsh, bay, and ocean habitats with varied marine, brackish, and freshwater conditions and moderate temperatures up to 20 °C (Grimaldo et al. 2017). Longfin Smelt typically spend 2 to 3 years in the Pacific Ocean before they migrate into freshwater regions of the upper estuary to spawn between the months of December and April. In spring, larval Longfin Smelt can be found in the northern Delta, Confluence, and Suisun regions. In the summer (between April and October), juveniles would migrate further downstream in the estuary to rear and grow to sub-adults. As sub-adults, growth in the estuary slows around fall and winter; some individuals then migrate to the ocean while others remain in the estuary (Merz et al. 2013; Tobias and Baxter 2021).

Laboratory studies and field surveys indicate that Longfin Smelt are sensitive to warm temperatures. Adult and sub-adult Longfin Smelt can tolerate water temperatures of 24 to 26 °C before mortality occurs (Jeffries et al. 2016; Davis et al. 2022). Higher field observations of larval Longfin Smelt at lower-than-average temperatures (Mahardja et al. 2017) are also consistent with studies that show reduced egg and larvae survival, growth, and performance at 15 °C (Yanagitsuru et al. 2021), and larval molecular and metabolic stress (Jeffries et al. 2016). Because Longfin Smelt have low temperature requirements at various life stages (e.g., spawning temperatures of ~7-15 °C), they likely do not have the physiological capacity to deal with warm and extreme temperatures of the Delta, and thus may shift toward or extend their time in the cooler bays or ocean (Wang 2007; Yanagitsuru et al. 2021). Thus, high heatwave frequency in the winter and summer, and the increasing trend in heatwave frequency, may further challenge Longfin Smelt and restrict the habitat they can occupy.

Nevertheless, Longfin Smelt demonstrate behavioral and spawning plasticity that may prove advantageous as high water temperatures, extreme heat events, and drought periods become more common. For example, higher temperatures have been linked to shifts in the timing of migration and seasonal distribution of Longfin Smelt across all regions of the estuary (Tobias and Baxter 2021). Longfin Smelt can also use tidally restored marshes and adjacent sloughs within the San Pablo Bay and South San Francisco Bay for spawning—displaying their capacity to spawn at higher salinities than previously thought (Grimaldo et al. 2017; Lewis et al. 2020). However, this plasticity will only prove beneficial if other conditions (such as food availability) do not degrade. For example, larval Longfin Smelt are highly selective feeders on the copepod *Eurytemora carolleeae* (Jungbluth et al. 2021) and may not be able to adapt quickly should this prey item decline further as the result of climate change or other related factors.

Chinook Salmon. The estuary supports four distinct runs of Chinook Salmon (fall-, late fall, winter-, and spring-run), all named after the timing of their adult upstream migration into freshwater. Habitat segregation and degradation from dams and other anthropogenic events have negatively affected these Chinook Salmon runs (Moyle 1995), leading to two runs in the Central Valley being listed under the federal and state ESA: winter-run and spring-run (Williams 2006). Today, fall-run is the most abundant Chinook Salmon run in the system (Williams 2012), with adults traveling through the Delta as they make their way upstream between July and December (warm period). Spring-run were once highly abundant throughout the Central Valley but are now limited to a handful of tributaries within the Sacramento basin and an ongoing population-restoration effort in the upper San Joaquin River. Spring-run also migrate through the Delta during warmer periods between March and September. While most juvenile Chinook Salmon migrate downstream and into the ocean within their first year, some remain in freshwater for a year and out-migrate as yearlings (Michel et al. 2015). Juvenile Chinook Salmon are typically observed in the Delta between October and June, with different out-migration windows depending on the run. During wet years, juvenile Chinook Salmon often benefit from inundation of floodplains such as the Yolo Bypass, where ample food leads to higher growth for rearing juveniles (Sommer et al. 2001).

Studies indicated that Chinook Salmon have an optimum performance range somewhere between 13 and 20 °C (Davis et al. 2022) depending on life stage and run type. In a laboratory setting, adult and juvenile Chinook Salmon can tolerate water temperatures up to 24 to 29 °C before mortality occurs, depending on acclimation (Zillig et al. 2023). However, the majority of field observations of Chinook Salmon occur at lower temperatures: <20 °C for adults and <18 °C for juveniles (fry or smolt) (Bashevkin, Gaeta, et al. 2022; Davis et al. 2022). The lower temperature thresholds observed in the field are consistent with studies that showed negative effects of temperatures >19–20 °C, including reduced growth and metabolic capacity (Zillig et al. 2023), impaired smoltification indices (Marine and Cech 2004) and decreased survival in saltwater (Clarke and Shelbourn 1985), as well as cellular and molecular stress responses (Tomalty et al. 2015). A study on juvenile Chinook Salmon in field enclosures within Suisun Marsh also found the greatest growth in the coolest habitat, where maximum daily temperature is 15.7 °C rather than 19.9 °C (Aha et al. 2021). There is also a growing recognition that Chinook Salmon exhibit run- and population-specific thermal tolerance, with winter-run Chinook Salmon experiencing greater growth rate decline relative to other runs at 20 °C, but also a greater ability to acquire tolerance when acclimated to higher temperatures (Zillig et al. 2023). This suggests that warming and extreme heat events will affect each population differently, and that the temperature-management approach may need to be run- or even tributary-specific. However, the increasing trend in heatwaves and the high heatwave frequency we observed in the summer will likely be detrimental to Chinook Salmon as they migrate through the Delta.

Steelhead. Steelhead are the anadromous form of *Oncorhynchus mykiss*. The Central Valley steelhead are currently listed as a threatened distinct population segment under the federal ESA. As part of the salmonid family, steelhead share many similar issues with Chinook Salmon. *O. mykiss* distribution today is a fraction of its historical range, and the species likely faces thermal challenges as California is the southernmost limit of its range (Lindley et al. 2006). However, *O. mykiss* differ from Chinook Salmon in that *O. mykiss* display a complex suite of life-history strategies, capable of being freshwater resident or anadromous, and can spawn multiple times throughout their lifespan. One aspect unique to *O. mykiss* that warmer temperatures and extreme heat events will affect is changes to the species' life-history expression (i.e., whether individuals become anadromous or freshwater-resident). Life-history expression of *O. mykiss* is a complex interaction between genetics and the environment. Higher rates of anadromy have been observed in systems with warmer and sometimes stressful temperatures, while residency appears to be more common in cooler and more stable systems (Sogard et al. 2012). However, juvenile *O. mykiss* may require water temperatures between 6.5 and 11.3 °C (Myrick and Cech 2001), and need to grow past a size threshold (Beakes et al. 2010; Satterthwaite et al. 2010) to successfully initiate and undergo parr-to-smolt transformation. These temperature requirements are consistent with the average field observations of steelhead in the Delta that occur near 12 °C (Bashevkin, Gaeta, et al. 2022; Davis et al. 2022). Although life-history expression may be temperature-sensitive, laboratory studies of wild juvenile *O. mykiss* suggest that the species demonstrates some local adaptation to warmer temperatures, as evident in the southern-most strain of the population in the lower Tuolumne River (Verhille et al. 2016). Juveniles from northern and southern strains generally can tolerate up to 24 to 31 °C, grow faster with warm temperatures of >18 °C, and maintain metabolic performance up to 22 to 24 °C (Myrick and Cech

2000; Verhille et al. 2016). It remains unclear whether climate change will favor anadromy or residency for *O. mykiss* that reside near the Delta, but the species' rate of anadromy will undoubtedly be affected in some manner by rising temperatures and increasingly frequent heatwaves.

Terrestrial Taxa

There are key parallels and differences between the aquatic and terrestrial ecosystems of the upper estuary. Terrestrial systems that surround the upper estuary will face similar challenges associated with warming: phenological and community shifts at multiple trophic levels, threatened and endangered species with limited capability to migrate into cooler regions (Halstead et al. 2010; Smith et al. 2018), and the continued expansion of heat-tolerant invasive species (Sandel and Dangremond 2012). However, relative to the aquatic habitat, the trajectories of the terrestrial systems that surround the upper estuary will likely be more directly influenced by how land will be used, managed, and regulated in the future. Even protected areas and conservation easements for wildlife—some of which are critical for bird conservation in the upper estuary (Dybala et al. 2023)—are often heavily managed in terms of their land use and freshwater flow. Meanwhile, most of the lands in the Delta are used for agriculture, which can interact with the aquatic and terrestrial ecosystems in various ways through pollination, pest control including use of pesticides, nutrient cycling and runoff, carbon sequestration, and water use (Power 2010). Crop yields are expected to decline as a result of climate change; however, technological improvements can partially offset these negative effects, and climate-change effects on California's water supply—rather than changes in temperature alone—are more likely to influence crop production (Medellín–Azuara et al. 2011).

Just as with their aquatic counterparts, some native terrestrial taxa at higher trophic levels will be negatively affected by the rising temperatures and increased variability of freshwater access. Listed species such as Salt Marsh Harvest Mouse (*Reithrodontomys raviventris*) and San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) have limited capability to disperse because of the lack of habitat connectivity (Smith et al. 2018; Rose et al. 2023). In contrast, birds are generally more mobile relative to other taxa and should encounter fewer barriers as they adjust their distribution and timing as a result of rising temperatures. Birds native to eastern North America have already shifted northward as more temperate conditions develop at higher latitudes (Rushing et al. 2020), and migration timing for nocturnal species within the contiguous United States appear to have shifted with warming (Horton et al. 2020). Nevertheless, birds have and will continue to be affected by rising temperatures and heatwaves. Migratory birds may experience temporal mismatch with their prey as they adjust their phenology, potentially causing population-level declines (Saino et al. 2011; Shipley et al. 2020). Extreme heat can be physiologically demanding for birds and affect their thermoregulation as well. Eggs will be increasingly exposed to sub-optimal or even lethal temperatures, though shifts in nesting phenology or nest-site selection (or both) may mitigate this (DuRant et al. 2019). Yet energy expenditure associated with parental care can also come at a high cost during warm conditions, likely leading to overall lower reproductive capacity (Nord and Nilsson 2019; van de Ven et al. 2020). While behavioral responses such as gular fluttering can be effective at relieving heat load through evaporative cooling, ~~it~~ also greatly increases rates of evaporative water loss and can increase risk of dehydration (McKechnie and Wolf 2010). This high thermo-regulatory cost may have caused the collapse of the bird community in the hot and dry Mojave Desert (Riddell et al. 2019). Increasing temperatures are also predicted to cause a reduction in body size; however, body sizes of birds in central California did not exhibit a clear trend, possibly because of climate variability (e.g., changes in precipitation, primary productivity, etc.) (Goodman et al. 2012).

Although we have focused mainly on the negative consequences associated with higher temperatures and heatwaves, it is worth noting that a number of terrestrial species in California, native or otherwise, are adapted to the extreme natural fluctuations in climate and their associated effects on water resources (Sandel and Dangremond 2012; Ball–Damerow et al. 2014). Some of these non-aquatic species may thrive under warmer conditions, and can more directly and unavoidably affect humans than aquatic taxa (e.g., the mosquitos *Aedes aegypti* and *Aedes albopictus*).

Human Effects

Heat is the leading cause of death among climate change-related disasters as well as some other devastating health effects (National Weather Service Weather Related Fatality and Injury Statistics). In California, we have already observed the effects of health-related outcomes such as dehydration and heat-related illness and mortality; however, the actual magnitude of heat-related mortality and morbidity is severely under-reported (Basu and Ostro 2008; Basu et al. 2012). Because there are no formal definitions for a heatwave or heat-related mortality in the United States, mortality and morbidity from heat are often only reported after heatwaves when no other cause of death is reported. Another reason for the under-estimation of heat-related health effects is that indirect negative health outcomes are often not considered. In California, increased risk of mortality and morbidity from cardiovascular, respiratory, diabetes, liver and kidney diseases, and gastrointestinal diseases have been reported during the warm season (Basu et al. 2008; Basu and Ostro 2008; Green et al. 2010; Ostro et al. 2010; Basu et al. 2012; Malig et al. 2019). There is also a large body of literature that links heat and adverse birth outcomes (Bekkar et al. 2020), such as pre-term delivery (Basu et al. 2010; Avalos et al. 2017; Basu et al. 2017), low birth weight (Basu, Rau, et al. 2018), stillbirth (Basu et al. 2016), and infant mortality (Basu et al. 2015). More recently, the connection between temperature and violence and mental health-related outcomes—such as homicides, suicides, and neurotic and psychotic diseases—have been found in California and elsewhere, (Basu, Gavin, et al. 2018; Clayton 2021). Vulnerability, however, varies by several factors such as race/ethnicity and age, with greater effects generally observed in non-white populations and for infants, young children, pregnant women, and the elderly. Employment type, socio-economic status, immigration status, and housing insecurity may also modify susceptibility among populations (Gronlund 2014; DSC 2021; Fong et al. 2022; Park and Pappalardo 2022; Schwarz et al. 2022).

Primary Heat Outcomes

Statewide health effect estimates from direct heat attributed to illnesses include dehydration, heat stroke, heat exhaustion, heat syncope (fainting), heat cramps, and related conditions with emergency room visits and hospitalization records. With the estuary bordering the agriculturally-rich Central Valley, morbidity from heat illness may increase as a result of both extreme heat events as well as generally higher outdoor temperatures. At the same time, however, because the Bay–Delta enjoys the “Delta Breeze” during the warmer parts of the year (see Temperature Drivers), areas where these winds are stronger (closer to the Carquinez Strait) may experience a greater cooling effect. On the other hand, residents living in these cooler areas of the Delta may have a more difficult time acclimating if an extreme heat event occurs due to the stagnant air, especially those in coastal areas with limited access to climate-controlled environments.

Interactions with Drought and Salinity

In addition to these more well-established links between heat and health outcomes, new emerging issues may affect or modify health risks in the Bay–Delta. Portions of the Central Valley included in the Bay–Delta may see a higher risk of coccidioidomycosis (Valley fever), a mycotic infection linked to drought (See SBDS Drought Chapter) and intense ground-warming as the result of extreme heat (Gorris et al. 2019; Pearson et al. 2019). Any ground-disturbing activity—such as construction, digging firebreaks, or tilling undisturbed soil—could expose residents and farmworkers to Valley fever. Pregnant women, immune-compromised individuals, and—for reasons that are unclear—those of Filipino and African-American ancestry are at increased risk of developing serious symptoms of the

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disease, including skin and brain lesions, leading to coccidioidal meningitis, a life-threatening condition. Extreme heat and drought can work interactively and also increase water salinity, which can pose health risks to people both directly and indirectly, and present a growing concern for the Bay–Delta region's drinking-water supply (DSC 2021). Some studies have indicated that ingesting water with a high salt content can lead to direct health complications, such as blood pressure elevation, which may lead to other complications (Khan et al. 2011; Nath et al. 2012; Pearson et al. 2024). High salinity in water also makes it unusable for agricultural irrigation (Pereira et al. 2019), which can then affect food availability and abundance, indirectly affecting residents' nutritional and dietary needs.

Vectors, Microbes, and Other Pathogens

Residents in the Bay–Delta could also have higher risk for other vector-borne diseases, particularly those attributed to invasive mosquitos, some of which tend to acclimate better to hot and high-salinity areas. Heat and high salinity can reduce the reproductive capability of native mosquitoes and allow non-native, more aggressive mosquitoes that tend to be more resilient in more extreme environments to thrive (Ramasamy and Surendran 2011; Multini et al. 2021; Pearson et al. 2024). Some of these species, such as the *Aedes aegypti* and *Aedes albopictus* (Asian tiger mosquito), serve as vectors for chikungunya, dengue, Zika, and West Nile viruses, and both of these species have been identified in the Bay–Delta's Sacramento region. *A. aegypti* has also been found in a number of Bay–Delta counties, including Contra Costa, San Joaquin, and Yolo (*https://www.cdph.ca.gov/Programs/CID/DCDC/Pages/Aedes-aegypti-and-Aedes-albopictus-mosquitoes.aspx*).

Heat and drought can also exacerbate HABs (see "Phytoplankton" section), which pose a health risk to Bay–Delta residents. When consuming seafood contaminated by toxins produced by these HABs, humans can experience severe illness. For instance, some *Pseudo-nitzschia* species can cause symptoms such as nausea, vomiting, and diarrhea at lower doses—and seizures, coma, irreversible memory loss (also known as "Amnesic Shellfish Poisoning"), and death at higher doses. Dinoflagellates such as *Alexandrium* can produce saxitoxins (paralytic shellfish toxins), which can lead to neurological conditions such as facial numbness, nausea, vomiting, respiratory failure, and death (Anderson et al. 2021). Both *Pseudo-nitzschia* and *Alexandrium* have been found in brackish to marine salinities in the estuary (Kudela et al. 2023). HABs can also pose a direct threat to human health through aquatic recreation, drinking water, consumption of plants irrigated with contaminated water, or respiratory exposure to aerosolized toxins (Kudela et al. 2023). In the estuary, freshwater HABs will more likely play a large role in human health effects, particularly from cyanobacteria. For instance, inhalation or ingestion of *Microcystis*—common in the Bay–Delta (Kudela et al. 2023)—may cause vomiting, nausea, headaches, diarrhea, pneumonia, and fever, while dermal contact can lead to skin rashes, burns, and blistering. Large doses can lead to severe liver damage (*Microcystis Toxic Blue-Green Algae* fact sheet; *https://oehha.ca.gov/media/downloads/ecotoxicology/fact-sheet/microfactsheet122408.pdf*). More information on HAB species, toxins, and drivers in the estuary can be found in Kudela et al. (2023).

Further research could identify specific vulnerabilities within estuary residents, particularly with even more emerging issues. Because some areas in the estuary include agricultural land, interactions between heat, other environmental exposures, pesticides, and microbes may play a role in population health outcomes. Farmers have introduced recycled or reclaimed water to reduce freshwater use in agricultural settings. At the same time, however, recycled high-pressure water spray and extreme heat in agricultural fields can aerosolize pathogens such as the bacterium *Legionella pneumophila* (which can cause legionellosis), and could pose a hazard to farmworkers or rural residents if sprinkling occurs during the hottest parts of the day and close to residences (Hamilton et al. 2018; Mori and Smith 2022; Pearson et al. 2024).

Chemical Volatilization and Drift

Outdoor temperatures above a certain threshold can lessen the potency of agricultural pesticides, thus requiring a larger volume of application. For instance, in areas where temperatures reach higher than 80 °F, many pesticides could become deactivated (Delnat et al. 2021). As a result, farmers may increase the volume of chemical application to offset the effect, potentially leading to higher exposure of pesticides for agricultural workers and even nearby communities, depending on wind direction and speed, and whether excess chemicals build up in water (Op de Beeck et al. 2017). As pesticides volatilize, the potential for spreading over a vast area also increases, again leaving farmworkers and nearby rural communities vulnerable to greater exposure (Delcour et al. 2015; Houbraken et al. 2016). Although there is some literature looking into these issues outside of the estuary and California, both of which output a large amount of agricultural production, there remains a dearth of information on these topics in the state.

Heat and Human Behavior

Heat and climate change can both lead to a longer warm season, and this extended warm season can affect human behavior, which can then affect people's risk to heat and climate-related health effects. As the warm season grows longer, allergen production is also expected to increase (OEHHA 2022). Because of extreme heat or allergen avoidance, some may stay indoors more often, leading to inactivity and exposing them to more indoor pollutants. This lack of exercise and social isolation could negatively affect both mental and physical health (McCormack et al. 2016; Evans 2019; Pröbstl–Haider et al. 2021). For others who can be outdoors, a longer warm season may increase overall time spent outdoors and improve their cardiovascular health through exercise, but their exposure to vectors would increase. For communities that lack access to air conditioning, a longer warm season may cause residents to participate in more water recreational activities, which in turn can lead to greater exposure to waterborne hazards, such as HABs (Young et al. 2022).

Vulnerability

Excess heat and associated increases in electricity demands have caused power outages all over California, including the estuary, increasing the risk for heat-related illnesses from inoperable air conditioning systems (Stone et al. 2021), as well as other health risks for those that need electricity for medical needs, such as refrigerated medicines or electronic medical devices (*https://www.fema.gov/blog/prepare-yourself-power-outage*). In addition, periods of extreme heat can be accompanied by poor air quality from the inversion layer that forms in the Central Valley (Grotjahn 2011), which could compound health risks, especially for those without operable air conditioning. The Bay–Delta also encompasses rural areas where people are socially isolated, and access to cooling centers can be limited. Furthermore, following a nationwide trend (Jiang et al. 2022), rural hospitals in operation have declined dramatically in California (*https://www.shepscenter.unc.edu/programs-projects/rural-health/rural-hospital-closures/*). For those living in rural areas, the lack of nearby emergency care poses additional health risk when heatwaves occur (Abbinett et al. 2020). Again, the Delta's agricultural workers will likely face the largest risk because they work outdoors, are economically vulnerable, and have poor access to healthcare as a result of rural locations as well as language barriers and lack of health insurance (Tigchelaar et al. 2020). Unhoused, immigrant, and low socio-economic-status populations also remain susceptible to increased heat effects because of such factors as more physical outdoor exposure, lack of translated information on heat avoidance and heat illness symptoms, and less disposable income to pay for air conditioning and other mitigating factors (Gronlund 2014; DSC 2021; Fong et al. 2022; Park and Pappalardo 2022; Schwarz et al. 2022). People of color, many of whom experience disproportionate cumulative effects from these other vulnerabilities, remain particularly at higher risk (Gronlund 2014; DSC 2021).

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CLIMATE CHANGE ADAPTATION AND FUTURE DIRECTIONS

In this article, we attempt to summarize the potential effects of warming and extreme heat events on the Delta ecosystem and communities (Figure 9); however, the effects we describe cannot be viewed in isolation. There will likely be interactions with other climate-change effects (e.g., increasing frequency of droughts, salinity intrusion from sea level rise) and actions intended to mitigate such impacts (e.g., water-management actions, tidal wetland restoration). The multivariate and interacting nature of these factors result in much uncertainty regarding the trajectory of the system. Nevertheless, some larger overarching trends were evident from our review (Figure 9). In the Delta ecosystem, we expect changes in phenology and a shift toward smaller-bodied species across all taxa. Meanwhile, a considerable number of non-native and cosmopolitan species that tolerate high temperatures are predicted to be resistant to or even benefit from a warmer climate. A number of these warm-tolerant species also happen to be eco-engineers capable of significantly influencing the make-up and structure of the ecosystem (Kimmerer et al. 1994; Hestir et al. 2016; Khanna et al. 2018). Warm conditions will also increase the likelihood of new species invading the ecosystem, which can lead to additional negative outcomes to both listed native species and humans. For humans, warming and extreme heat events will threaten the health and welfare of residents in the upper estuary. High temperatures are associated with wide-ranging health issues, from direct effects such as dehydration and heat exhaustion (Ostro et al. 2010), to other adverse health outcomes such as lower birth weight (Basu, Rau, et al. 2018), mental health problems, and violence (Basu, Gavin, et al. 2018; Clayton 2021).

Warming associated with climate change is a global issue that cannot be resolved effectively at a local level, because atmospheric influences remain the primary drivers of water temperature in the estuary (Vroom et al. 2017). Nevertheless, adaptation strategies for climate change can be developed locally, since each system may require specific tools and actions. For more complete information on the subject, we direct readers to the wealth of literature that exists on climate-change adaptation strategies (e.g., Keim 2008; Stein et al. 2013; Hyun et al. 2021), but here we provide several concepts and strategies we believe are worth highlighting for the upper estuary.

When minimizing the health risks and effects of prolonged heat exposure for humans, increasing awareness of the issues and solutions can be the first hurdle (Ittefaq 2024). Thus, it may be important to develop public education campaigns and heat warning systems to inform people about the risks of extreme heat and how to protect themselves. In urbanized areas, cooling centers and other climate-controlled public spaces can be key in providing relief during heatwaves. There may also be opportunities to increase green spaces in urbanized areas to provide more shading and reduce urban heat island effect. To minimize heat exposure and subsequent infection of *L. pneumophila* of agricultural workers, timing for sprinkling can be shifted to cooler parts of the day, personal protective equipment can be used to reduce inhalation, and crops can be planted further away from local communities (Hamilton et al. 2018).

To help preserve the native biodiversity of the upper estuary, Sommer et al. (2024) provided a comprehensive list of potential actions and tools to help combat climate-change effects. Actions that address issues directly related to warming conditions and heatwaves include flow and food augmentation, structures that can act as temperature refuge, and assisted evolution. The relationship between water temperature and discharge from reservoirs in regulated rivers of California is relatively well-understood (Daniels and Danner 2020); less so for the upper estuary. There is evidence suggesting that flow can affect water temperature in the estuary (Vroom et al. 2017; Bashevkin and Mahardja 2022); however, the amount of flow required to provide a meaningful temperature benefit for fish species in the Delta has not been quantified. Certain habitats or structures can potentially serve as thermal refuge for coldwater species. Riparian shading, tidal wetlands, and stratified deep channels can moderate water temperatures in the upper estuary to some extent (Greenberg et al. 2012; Enright et al. 2013; Mahardja et al. 2022). For forage fish species in the estuary such as Delta Smelt, warmer water temperatures mean higher energy requirements to maintain bodily functions, and actions that lead to higher food availability and/or quality can help mitigate temperature stress (Smith and Nobriga 2023). Lastly, assisted evolution techniques such as selective breeding, hybridization, and genetic engineering have been suggested as potential strategies to allow declining coldwater species to survive warm conditions that they would otherwise not be able to tolerate.

The potential strategies listed above are not necessarily recommendations. Some of these actions may face technical, financial, logistical, legal, or even ethical challenges. Studies are needed to identify and evaluate the challenges for each of the possible strategies we identified. The development and implementation of a climate-change-adaptation strategy will likely require many considerations, such as the uncertainty surrounding the efficacy of the actions, the possible social resistance to a new solution, fairness and equity, and trade-offs among priorities.

Overall, our results indicate widespread vulnerability to temperature increases in the Bay–Delta ecosystem and its residents. Although decreasing global greenhouse gas emissions remains our best option to combat climate change and the resultant temperature increases, successful adaptation to warming and heatwaves will require actions at multiple scales.

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